The foraging economics of honey bees in almonds

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Selected Paper prepared for presentation at the Agricultural & Applied Economics Association's 2011 AAEA & NAREA Joint Annual Meeting, Pittsburgh, Pennsylvania, July 24-26, 2011

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Abstract: We develop a model of honey bee foraging behavior that can be used to simulate crop yields as functions of honey bee densities. These yield functions help us understand the economic behavior of growers who rely on bees for pollination. One important simulation result for the case of almonds is that the production function facing growers is close to one of fixed proportion in pollination input. Accordingly, the modeling of the foraging behavior of bees provides an explanation for the observed lack of variation in pollinator use and shows how the behavior of bees and growers are connected.

In the few months following the spring of 2007, all ten of the most circulated newspapers in the United States published alarming articles on the mysterious disappearance of domestic honey bees, spreading widely the idea that domestic bees were declining. Claims that populations of wild pollinators were also threatened further reinforced the notion of an ongoing pollinator decline. The causes of pollinator declines were and remain the subject of some debate, which often relate to agricultural practices and the intensive use of natural resources. The consequences of pollinator loss on the availability of food were and still are almost unanimously predicted to be catastrophic.

Since, a more thorough analysis of the magnitudes, causes, and consequences of these pollinator declines has been under way. Biologists have provided the main thrust of this research effort. The economic aspects of pollination in agriculture have received little attention. Yet, an economic analysis of the consequences of pollinator declines is important because the impact of increases in the scarcity of pollination services on food prices and quantities hinges on the economic response of crop growers to increases in the scarcity of pollination services. This paper contributes to remedying the lack of economic analysis of the derived demand for pollination services as inputs for crop production.

Olmstead and Wooten (1987) noted two decades ago that economists had paid little attention to pollination services as*an input* to agricultural production and their observation still holds today. Aside from Olmstead and Wooten (1987) and the appendix of Rucker, Thurman, and Burgett (2008), the contributions on the economics of pollination focus on the supply of bees by the beekeeping industry or on the existence of markets in which beekeepers sell the pollination services of

their bees to crop growers.[1] To our knowledge, Rucker, Thurman, and Burgett (2008) is the only contribution which discusses explicitly and in some detail the economics of pollinators as inputs.

In the recent literature that addresses the impact of the declines of both managed and wild pollinators on consumer welfare, the economic behavior of crop growers is generally ignored. The relationship between the number of pollinators available and the quantity of crop produced is limited to indicators of pollination dependence. These indicators reflect the reproduction biology of the crops and are estimates of the share of yield loss that would follow from the absence of pollinators. For instance, Gallai et al. (2009) who review values in the literature, report that yields of strawberries would decrease by 10 to 40 percent. The reliability and interpretation of these dependence ratios remain subject of debate among biologists (Gallai et al., 2009; Allsopp, De Lange, and Veldtman, 2008). For economic analysis, these ratios can be used as a measure of the drop in output resulting from the interruption of the use of any pollinators as inputs, keeping the use of all other inputs constant. Accordingly, these ratios provide information about the production functions of crops that use pollinators but they do not incorporate the economic behavior of producers and the market adjustments of commodity prices. By and large, the economic tradeoffs involved in the production of the crops that require pollination services remain to be identified and quantified.

One of the consequences of the lack of attention devoted to the use of pollination services in agriculture is the absence of data on input use. There is no record of the number of hives that provide pollination services in the United

[1]Most of the interest from economists in pollination was triggered by the theoretical problem of externalities, rather than the empirical importance of pollination services as a crop input. The central result of this small literature is that pollination markets do seem to provide efficient incentives for both beekeepers and growers.

States, let alone a history of their use for individual crops.[2] For most crops, the only data available are the rental prices of hives for one or two decades and recommendations on the number of colonies that should be placed on an acre of crop in order to achieve sufficient pollination.

For California crops, the best two sources of data on commercial pollination are beekeeper surveys from the Honey Bee Laboratory at Oregon State University and the California State Beekeeper Association. They both provide average rental prices of hives, or pollination fees, by crops for the last couple of decades. Summary results of surveys are published for instance in Burgett (1999) and Burgett (2007). In addition, the Oregon survey data include information on both the number of hives and the number of acres serviced for each pollination contract which allows Rucker, Thurman, and Burgett (2008) to estimate changes in hive densities.

Although these survey data provide the only existing time series of pollination fees, they are ill-suited for the empirical analysis of pollination input use. Hive densities per acre cannot be inferred from the survey data of the California State Beekeeper Association. The Oregon survey data provide information on hive densities but are based on the responses of 17 Oregon beekeepers representing 37,095 hives (Burgett, 2007). Both the small size and the geographic bias of this sample limit the robustness of inferences drawn for larger regions such as California.

The recommendations of experts for hive stocking densities provide a second source of information on pollination input use. McGregor (1976), who reviews pollination recommendation for most of the crops cultivated in the United States, remains the reference for many crops. However, these recommendations are only

[2]There are two sources of hive counts for the United States. One is the annual Honey reports where only hives producing honey are accounted for. Another source is the Census of Agriculture but it only provides the total number of hives without distinction of their use.

indirect measures of input use and their accuracy depends on how closely recommendations are followed by crop growers. Furthermore, such recommendations are not conditional on economic considerations such as pollination fees.

This paper explores the economics of pollinator use in detail with the help of a simulation model which estimates almond crop revenues per acre as a function of pollinator use. The results of this model provide a third source of information that complements survey data and expert recommendations and provides new insights on the economic nature of pollination use in agriculture.

The importance of almond pollination in California

We use the case of almond pollination in California to contribute to bridging the gap between pollination ecology and the economic behavior of growers. Almonds are the best place to start investigating the economics of pollinator use for three main reasons.

First, the pollination ecology of almonds and the foraging behavior of honey bees are both better documented than for other crops and pollinators. Almonds are, along with alfalfa, one of the crops where practices designed to increase pollination success have received the most attention from agronomists. Also, commercial almond pollination involves the foraging behavior of a single species, honey bees, in homogeneous monocultures. In 2007, $640,000$ acres of almond orchards were pollinated by honey bees.[3] Using an estimate of 2 to 2.5 hives per acre, almond pollination required 1.3 to 1.6 million hives. Spatial and temporal factors contribute to making this pollination relationship exclusive on both sides. Most orchards are spatially segregated from both habitat of potential

[3] 2009 California Almond Forecast, National Agricultural Statistics Service of the U.S. Department of Agriculture (NASS).

alternative pollinators and from plants or crops that could be visited by honey bees.[4] The segregation is temporal as well, since almonds bloom earlier than most other crops and plants in the region, and before the emergence of most native pollinators. The ecology, and in particular the foraging behavior of honey bees is well documented. The eco-physiology of almond trees, including their reproductive stage has also been well studied. Accordingly, almond pollination lends itself to tractable ecological modeling.

Second, almond pollination is important beyond its illustrative value for the understanding of pollination markets. In 2007 the almond crop attracted more than half of the 2.4 millions of commercial hives in the country. Pollinating fees from almonds represent about a third of the $580 million of revenues of the beekeeping industry.As a result, the demand for hives to pollinate almonds is likely to be an important driver of pollination markets for the near future.[5]

[4]Kremen et al. (2007) document a case in the Capay Valley where surrounding natural habitat sustains populations of potential pollinators other than managed honey bees. Most almond acres however, are more distant from such habitat and managed honey bees are virtually the only insect pollinating almonds in the San Joaquim Valley, which contains 80% of California's almond acreage. The only other species of managed pollinators used for almond pollination is the leaf-cutter bee, for which research is still ongoing and adoption is at an early stage (Kremen et al. (2008)).

[5]The revenues of the beekeeping industry include pollination fees, honey sales, and revenues from other bee products such as wax. The Honey report of the National Agricultural Statistics Service (NASS) of the USDA only provides data on hives which produce honey and does not report pollination revenues. In 2007, there were 2.44 million hives nationwide that produced on average $62 of honey. We use the average annual rental income reported by Burgett (2007), which was $176 per hive in 2007, and multiply it by the number of hives from the NASS data to estimate the pollination income of the industry. There are no available data for the hives that do not produce honey, although their numbers may be considered relatively small in first approximation. In contrast, Burgett (2007) surveys beekeepers in the Northwest region of the United States, most of whom participate in almond pollination. The actual rental revenue of the 1 million hives that do not go to almonds is likely to be lower. The average fee for almonds was $137 per hive which multiplied by 1.4 million hives, provides an estimate of $192 million for the almond pollination fee revenue. We do not include the value of queens and bee packages as outputs of beekeeping since they are inputs for pollination and honey operations.

Third, honey bees used for almond pollination have become more expensive. The pollination fees paid by almond growers for hive rentals have more than tripled during that period as shown in table 1.[6] The rise in pollination costs for almonds is unprecedented and provides an opportunity to observe the behavior of growers facing a drastic increase in the relative scarcity of pollinators.

The rule of thumb for almond pollination

Rucker, Thurman, and Burgett (2008) find some evidence that the growers of most if not all crops have maintained a constant number of hives per acre despite variations in their rental prices. In their economic analysis of the beekeeping industry, Willett and French (1991) also briefly mention the fact that they observe no variation in hive use with changes in the prices of pollination services.[7]

My conversations with farm advisors, almonds growers, and beekeepers revealed that about two hives per acre has been used as a rule of thumb across the industry for the last three decades at least.[8] The consensus is not complete however, since a few experts such as Joe Traynor and Frank Eischen argue that one strong hive per acre may be enough.[9]

The hive densities found in the cost and return studies of the University of California Cooperative Extension provide a contrasting picture (see table 1). These studies represent the opinion of farm advisors and describe practices that

[6] Almond growers who own hives are rare but there is anecdotal evidence that they stock their orchards at a similar density (Dan Cummings, personal communication).

[7] Willett and French (1991) do not provide any explanation since their objective is to built a general model of the beekeeping industry with no particular emphasis on pollination and no explicit treatment of the demand for pollination services.

[8] The densities reported in table 1 are obtained from interviews of experts in the industry and are expected to be similar to the values obtained from my own communications with beekeepers and almond growers.

[9] Joe Traynor is a bee broker in California and Frank Eischen is a research entomologist at the Agricultural Research Service of the USDA.

are considered typical for the crop and area. The hive densities used in these studies show no clear relationship with changes in pollination fees or input to output ratios.[10]

Overall, there is no clear evidence that orchard stocking rates have decreased despite the recent rise in rental prices of hives for almonds. The rule of thumb of two hives per acre remains a commonly cited practice.

In addition, several changes in the production practices of almonds also affect pollination practices. In particular, recommendations for honey bee use are generally not made only in terms of hive densities but also include the size of the population inside the hives, or "hive strength". Indeed, the foraging activity of hives increases with colony size as shown by measures of pollen collection and by observations of flight activity (Sheesley and Poduska, 1970). Furthermore, specialization of bee workers as well as reductions of heat losses are the source of economies of scales that are visible in the relationship between hive size and foraging activity (Danka, Sylvester, and Boykin, 2006). Although there is some variation among experts about best pollination practices for almonds McGregor (1976) is a widely cited source and after reviewing the literature on almond pollination McGregor argues that:

> The studies indicate that at least two to three strong colonies per acre may be required for maximum production of almonds. The colonies should be distributed within the orchard in small groups one-tenth mile apart. Each colony should have at least $800\ in^2$ of brood and a cluster of bees that covers most of the frames in a two-story deep-frame hive.

[10] This lack of relationship remains when output prices are lagged to take into account the fact that producers make input decisions based on expected prices.

Although there is some variation across professionals on the method for measuring the size of colonies in hives, most measures are based on counting the number of frames in a hive that are covered by bees. Standard commercial hives are made of two or more stacked wooden boxes, or stories, containing each 8 to 10 frames hanging vertically. Bees generally form a spherical cluster in the hive. As a result, opening the hive and counting the number of frames that are covered by the cluster provides an estimate of the volume of the cluster and of the number of bees in the colony. Variations in the methods of estimation of hive strength are related in particular to the way partially covered frames are counted and added up.

As opposed to the recommendation for the number of hives per acre which has remained about constant at about two since Tufts (1919), the recommendation for hive strength has shown more visible variation over the years and across experts. According to Sheesley and Poduska (1970), the California Beekeepers Association defined the minimum standard for hive size as 4 frames of bees in 1968.[11] In table 1, we report the hive densities provided by the cost of production studies of the University of California Cooperative Extension. Despite the fact that there does not seem to be a single standard in the industry today, 6 frames of bees are generally considered a minimum for almonds. According to my conversations with almond growers and beekeepers, 8 frames of bees is considered a good pollination unit for almonds.[12] Although it did not seem to be often the case forty years ago according to Sheesley and Poduska (1970), pollination contracts now often include

[11] The standard also requires the presence of a laying queen whose activity is revealed by the presence of frames of brood.

[12] Some beekeepers and bee brokers offer pricing schedules based on frame counts per acre rather than hives (Mike Russo, personal communication).

provisions on hive strength and third party certification is provided by private and county inspectors.

The extent to which hive sizes may have increased in the last few decades is difficult to ascertain because data on frame counts are even scarcer than hive counts.[13] In addition, the size of hives in spring shows large variation depending in particular on weather conditions during the previous year, as shown in Sheesley and Poduska (1970). It is quite likely that the size of hives used for almonds has increased on average by one or two frames at least and that contracts more often include quality standards than forty years ago. However, this change has been gradual and moderate, and seems insufficient to explain the recent and abrupt hike in the rental price of hives for almond pollination (see table 1).

Another change that must be taken into account in the analysis of the response of hive use to price changes is the change in input mix. Although the ratio of land to hives has remained constant, the ratio of trees and other inputs to bees has not. Between 1995 and 2008, tree density has increased from 93.7 to 107.0 trees per acre on average.[14] In parallel, the yield per acre has also increased, due to a higher tree density, but also to improvements in varieties, planting patterns and other management practices. Almonds are an alternate bearing crop and their yield shows great variation from year to year. Nevertheless, a look at average yields from the last fifteen years in table 2 shows a significant increase. There is no clear trend in the price of almonds and therefore the gain in revenue per acre is mainly due to the yield increase. The values of shares of pollination costs in total revenue

[13]One promising lead for data is the records of county inspectors. Further work is required to find how comprehensive the records of hive inspections are and whether they are accessible. Also, such data is likely to present some selection bias since inspections for hive strength are not mandatory but provided upon request and for a fee.

[14]Source: 2009 California Almond Objective Measurement Report, NASS, USDA. Available at http://www.nass.usda.gov.

calculated in table 2 are smaller than the shares in operation costs but show a similar trend.[15] Although the combination of yield increase and fixed stocking densities means that fewer hives are used per pound of almond, the magnitude of this change is dwarfed by the large increase in the ratio of input to output price for hives. As a result, the demand for hives for almond pollination seems to have been very inelastic for the range of price changes of the last couple decades.

Explaining the rule of thumb

Our objective in this paper is to find hypotheses that explain the the fact that only small variations in beehive use exist in almonds. The most obvious hypothesis is that hives are a required input for almond production, or equivalently that the production function for almonds displays fixed proportions in hives and other inputs. Given the lack of sufficient data on hive use by almond growers, an estimation of a production function from time series or cross section data on yield and input use is unfortunately not feasible. Instead, the only available information comes from field experiments and the agronomic literature on almond pollination. The most important result of this literature is that all varieties of almond trees are self-incompatible and set nut only if pollen from compatible varieties is deposited on the receptive stigmas of their blossoms. The pollination requirements of individual blossoms can be fairly easily ascertained by manual pollination and bags to exclude visits from pollinators. At the scale of an individual blossom, pollination services are therefore a fixed proportion input without which no nut can be obtained. Because a nut drop naturally occurs after pollination in almonds, authors argue

[15] Although the two tables use data from different sources, the main difference in the values of shares in their last columns is due to the difference between revenues per acre and operating costs per acre.

that growers should try to make sure that all blossoms are pollinated (McGregor, 1976).[16] This strict requirement explains why most authors recommend large populations of bees in orchards without consideration for the economic cost of honey bees.

Yet, the relationship between the density and size of hives as inputs and yield of an entire orchard need not be itself one of fixed proportions for two reasons.

First, although the pollination requirement is strict for each blossom, heterogeneity among blossoms will make the aggregate nut set response to pollination services smoother.

Second, the relationship between the number and size of hives placed in an orchard and the amount of pollination services received by blossoms must also be taken into account. DeGrandi-Hoffman, Roth, and Loper (1989) develop an simulation model of almond pollination that predicts almond yield as a function of honey bee density. Their predictions are based on empirical relationships calibrated with data from an experimental orchard. However, their approach does not rely on a model of foraging behavior of honey bees and does not specify how hives allocate the foraging efforts of their bees. In particular, it does not take the spatial aspect of hive foraging behavior into account. Since bees forage from and return to their nest, a gradient of flight cost makes blossoms close to hive more likely to be pollinated than distant ones.

Below, we develop a model of yield response to hive stocking density that couples a model of honey bee foraging behavior with a model of almond flowering based on DeGrandi-Hoffman, Roth, and Loper (1989). The release of pollen by blossoms determines the availability of forage for bees and the receptivity of their

[16] In apples for instance, excessive fruit set requires fruit thinning (Dennis, 2000).

stigmas to pollen deposition determines the nut set and resulting yield. Honey bees forage so as to maximize the hive's returns to foraging, which depend on energy cost of flying to and from blossoms and the density of pollen available on the blossom. The model is spatially explicit, which allows me to predict the patterns of foraging efforts and resulting pollination services in orchards. We take into account the competition of hives for forage. We simulate the pollination and yield outcomes as a function of the relative densities of hives and blossoms, the spacing of hives, the size of the hives and their nutritional needs as well as other variables that farmers cannot adjust, such as weather conditions. We find that heterogeneity in blossoms, mainly due to the timing of their maturation as well as the foraging behavior of hives smooths the relationship between hive inputs and almond yield to some extent .

In addition to the shape of the production function for almonds, other hypotheses can be proposed to explain the limited of response of hive densities to pollination fees. Rucker, Thurman, and Burgett (2008) propose two hypotheses.

First, Marshall's third law for the derived demand for an input states that the elasticity of the derived demand for a factor is an increasing function of its share in production costs. In addition to the fact that the law is in fact not always true the share of pollination fees in production cost has gradually increased over the years reducing thereof the explanatory power of this first hypothesis (see table 1). [17]

[17]The easiest way to see that Marshall's third law is not always true is to use the derivation of the elasticity for the derived demand in Muth (1964) and take its derivative with respect to the cost share. Muth finds the expression of the elasticity to be $\frac{\sigma\eta-((1-k_B)\sigma-k_B\eta)e_A}{k_B-(1-k_B)\eta+e_A}$ where σ is the elasticity of substitution between the two inputs, η the elasticity of demand for the output, k_B the cost share of the input of interest B, and e_A the elasticity of supply of the other input. The derivative with respect to k_B is $\frac{(\sigma+\eta)(e_A(\sigma-\eta+e_A)-\sigma\eta)}{(k_B-(1-k_B)\eta+e_A)^2}$. Since η is in general negative and all other parameters positive, the sign of the derivative depends on the sign of $(\sigma+\eta)$. Marshall's third

Second, Rucker, Thurman, and Burgett (2008) argue that growers do not know with precision how bee pollination benefits their crops and that they therefore follow the advice of farm advisors whose recommendations are not conditional on economic factors.[18]

This last hypothesis derives from the pervasive notion that the activity and benefits from the foraging of honey bees are costly to measure. A similar idea underlies Meade's famous example of "unpaid factors" as a type of externality existing between beekeepers and apple-growers. Yet, prohibitive costs of acquiring information on individual production functions are not sufficient to explain the behavior of growers. If anything, it displaces the question to one about the economics of collective information acquisition. If honey bee densities are determined by the recommendations of experts, understanding the response of pollinator use to prices hinges on understanding the production of information by these experts.

The results of the spatial model of foraging behavior developed below show and quantify the extent to which the diffusive nature of pollination makes it difficult for individual growers to learn about the relationship between hive use and yield (see section . The next three sections present the model of foraging behavior of hives in commercial almonds orchards. First, we develop a model of hive behavior in a landscape where a given stock of pollen is distributed homogeneously in space at the beginning of the foraging period after which it is progressively depleted the foraging of bees. The following section extends the model to allow the pollen to be

law is true when the elasticity of substitution between factors is larger in absolute value than the elasticity of demand for the output.

[18]One further hypothesis that deserves to be mentioned is the problem of strategic behavior among growers in the presence of externalities. With diffusion of bees, growers have incentives to keep their stocking practices undisclosed to either protect themselves from free-riding or to free-ride. This hypothesis, in addition to being somewhat convoluted can only be tested with indirect data on hive rentals and acreage.

released progressively during the early part of the foraging period and to depreciate when not collected by bees. Section shows how this model of foraging model can be combined with a more elaborate model of the dynamics of pollen release and blossom development in almonds. Finally, the yield function simulated by the full model of bee foraging in an almond orchard is used to understand the economic behavior of almond growers and explain the rule of thumb described above.

A spatial model of foraging behavior of hives

With ants, honey bees are the epitome of social organization in insects and their behavior is best understood in the light of selection at the colony level (Seeley, 1997). This is particularly true of their foraging behavior, which involves specialization of workers and information sharing. For honey bees, von Frisch (1967) initiated a large literature on the allocation of forager efforts among sources of different proximities and qualities. He identified the waggle dance as a central mechanism of information sharing and coordination.[19] In a nutshell, when returning from a valuable forage source, workers indicate both its location and value by performing a waggle dance. The orientation of the dance communicates the direction of the source relative to the hive and its duration and repetition the profitability of the foraging trip to that source.

The number of workers that are recruited to each available source depends on the size of the idle forager population that can be recruited and the relative intensity of the dancing signal of each source. Some proportion of workers, called

[19]The bee dance remained for a time source of controversy and was the ground for a famous confrontation between von Frisch and Adrian Wenner (Munz, 2005). However, Riley et al. (2005) and others have since established that the dance does reveal information on source quality and location to recruits. Odor cues left on flowers also play a role in information sharing but are not exclusive to honey bees (Goulson, Hawson, and Stout, 1998).

scouts, find new sources by foraging independently of this information. Seeley (1995) provides a comprehensive description of this coordination mechanism and the foraging behavior of colonies. Empirical observations show that colonies are capable of rapidly adjusting their foraging efforts with changes in source distribution and quality. Not only do they allocate forager force according to the nature, quality, and distance of sources, but they also respond to changes in internal variables such as feed needs and storage levels of nectar, pollen, and water (see for example Dreller, Jr., and Fondrk (1999)). Contributions such as de Vries and Biesmeijer (1998), Bartholdi et al. (1993), and others have developed agent-based models that use behavioral rules of individual bees in order to replicate the observed allocation of foraging efforts of hives. They find that the foraging efficiency resulting from the heuristic behavior of colonies is comparable in magnitude to that of a theoretically optimal allocation.[20] Following this literature, we assume that the foraging behavior of individual bees maximizes the colony's objective function, the specification of which we now discuss.

A currency for foraging efficiency

The objective of the foraging theory literature is to derive foraging behaviors that are consistent with natural selection. Pyke (1984) argues that the validity of foraging models depends in particular on the choice of fitness currency and physiological and ecological constraints that limit the range of possible behaviors. Cresswell, Osborne, and Goulson (2000) develop an economic model for animals foraging from a central place, or nest, and use two alternative currencies for source choice: the rate of net energy intake and the net energy gain, which differ regarding

[20]For a discussion of the emergence of the scout-recruit system in colonies see Seeley (1997) as well as Anderson (2001)

the implicit value of time. For honey bees, Seeley (1995) presents experimental evidence showing that colonies allocate their foraging effort according to net energy gain. First, the ability of hives to store both pollen and nectar (in the form of honey) in their combs increases the payoff from waiting for sources that hive high energy gain relative to the cost of foraging on them. The payoff of this waiting strategy is further increased by the ability of hives to rapidly detect and exploit new highly profitable source. Finally, Neukirch (1982) finds that the life span of workers is not fixed but in part determined by their foraging effort. As a result, the cost of an idle foraging force is low. The fitness of a hive, constrained by its energy budget rather than by time, is maximized by a forage allocation that follows the net energy benefit criteria defined by the ranking of forage sources according to the following ratio:

$$\frac{EnergyGain - EnergyCost}{EnergyCost}. \tag{1}$$

However, when forage is scarce, stocks are low, and hive feeding needs are high, allocating foragers to sources according to their rate of net energy intake:

$$\frac{EnergyGain - EnergyCost}{TimeCost}. \tag{2}$$

increases the fitness of the hive. The mechanism of adaption of foraging allocation criteria is not fully elucidated. We assume here that in commercial almond orchards hives behave according to the net energy benefit criteria. However, this assumption turns out to be relatively innocuous because both criteria lead to similar allocations of foraging effort with the particular parameters of commercial almond orchards.

The gains and costs from foraging depend on the nature of the source. Nectar provides energy and pollen, which is mainly consumed for bee rearing in

the hive and is the main source of proteins. In almonds, honey bees forage for both pollen and nectar and a fraction of the active foraging population specializes on each source.[21] Assuming that the behavior of these two populations can be treated separately allows me to model only the bees foraging for pollen. This simplification is innocuous when bees foraging for nectar do not significantly participate in the removal and deposition of pollen, which is the case in almonds. The shape of almond blossoms which contain both pollen and nectar makes it possible for bees foraging for nectar to 'side-work', collecting nectar without touching anthers or stigmas (Thorp (2000);Thomas Gradziel, personal communications). This simplification enables to specify gains and costs of foraging for pollen only.

Furthermore, we assume that the size of the load collected by each bee during each foraging trip is fixed. The cost of a trip is given by the sum of the energy cost of flying to and back from a source, the cost of collecting a load at the patch, and the cost of discharging the load at the hive.[22] The cost of foraging on patch i is

$$C_m(i,t) = MR_f \frac{2d_i}{v} + MR_c s(P_{i,t}, F_{i,t}) + MR_u UnloadDuration \tag{3}$$

where d_i is the distance from the hive, $P_{i,t}$ is the amount of pollen and $F_{i,t}$ is the number of blossoms in patch i at time t, v the speed of bees, $UnloadDuration$ the time required for unloading.[23] MR_f is the metabolic rate for flight, MR_c the metabolic rate for collection, and MR_u the metabolic rates for unloading, all in Joules per second. The time in seconds required to collect a load, $s()$, varies with

[21] Honey bees also forage for water and resin (propolis). See Seeley (1995) for a description of the specialization of workers.

[22] We implicitly assume a fixed conversion rate between energy value and nutritional value.

[23] To avoid confusion, we chose the letter "B" to designate variables related to bees, and the letter "F" for flowers.

the density of pollen. Seeley (1994) provides empirical estimates of metabolic rates. Because almond orchards can be considered homogeneous in the density of blossoms, $B_{i,t}$ is equal across all sources and the i index can be dropped. The speed of flight and energy cost depend in theory on the size of the load. An unloaded bee weights approximately 75mg, a pollen load 15mg, and a nectar load 50 to 60mg (Seeley, 1994). Seeley (1994) measures only small differences in flight times from and to the source and the load does not seem to slow the bee. The difference in energy cost between the two legs of the trip is therefore mainly due to differences in metabolic rates. This difference is small when the load is relatively light, as is the case with pollen.[24]

The specification of the time cost of collection $s()$ is the most challenging of the three terms of foraging cost because it accounts for a more complex behavior. The foraging behavior of individual bees is the subject of a large literature (see for example Thorp (2000) and Thomson and Goodell (2001)). In particular, the cognitive behavior of bees has received wide attention (Dukas and Visscher, 1994). Here, we simply assume that the time required to collect a given load is inversely proportional to the average density of pollen per blossom. This specification is valid when the size of load collected is fixed, the duration of a visit to a single blossom is fixed, bees visit the average blossom in terms of pollen content, and they collect a fixed proportion of the pollen available on each visited blossom. Specifically,

$$s(P_{i,t}, B_t) = \frac{LoadSize}{CollectionRate P_{i,t}/F_t} VisitDuration \tag{4}$$

[24]Seeley (1994) uses $MR_f = 0.00287M^{0.629}$ and $MR_c = MR_u = 0.00248M^{0.492}$ which are derived from oxygen consumption measurements and where M is the body mass including load. However, when foraging in almonds, bees have to fly from blossom to blossom which is likely to increase the metabolic rate of collection compared to Seeley's experimental situation where bees can walk from blossom to blossom.

where *CollectionRate* is the proportion of pollen collected from a blossom for each visit, *VisitDuration* its duration, and *LoadSize* the total load of a bee for each foraging trip.[25] Because of the morphology of blossoms and the adaptive behavior of honey bee to such morphology, the values of these three parameters are specific to insect-plant pairs. Thomson and Goodell (2001) provide estimates of the proportion of grains of pollen removed by honey bees on their first visit to a blossom, as well as the duration of these visits.

The difficulty of measuring pollen flows without altering bee behavior has limited the extent and precision of such quantitative measurements and an important limitation of the empirical estimates provided by Thomson and Goodell (2001) is that they do not allow for changes in visit duration and amount of pollen collected per visit as the amount of pollen available in each blossom decreases. Our specification is subject to this limitation and collection rate and visit duration are held constant.

Since we assume a fixed load size the nutritional or energy gain from each foraging trip is constant both across sources and across time on each source. As a result, ranking sources according to the criteria in equation 1 is equivalent to ranking according to the inverse of their respective foraging cost. The advantage of this simplification is that it circumvents the difficulty of converting the gain of each load from nutritional value to energy value. When the foraging gain is constant across sources, the ranking of sources according to the ratio of equation 1 is the same as the ranking of source by decreasing foraging cost as given in equation 3. Using the specification of the collection time $s()$ from equation 4, the complete

[25]The values of the model's parameter are reported in table A.2.

foraging cost of equation 3 can be rewritten as:

$$C_m(i,t) = MR_f \frac{2d_i}{v} + MR_c \frac{LoadSize}{CollectionRate P_{i,t}/F_t} VisitDuration + MR_u UnloadDuration. \tag{5}$$

This expression of the foraging cost of each source determines the source on which each bee forages and it is a function of two variables, the distance between the source, d_i, and the hive and the amount of pollen at the source, $P_{i,t}$.

The timing of bee foraging and forage depletion

The foraging activity of honey bees is limited by the weather. Bees do not forage and instead remain inside the hive whenever temperatures fall below 59°F, wind reaches more than 10mph, or rain occurs. The number of foraging hours varies with time and across the Central Valley of California. The average flight time for the almond seasons between 1996 to 2006 for the northern section of the valley was 58.1 hours according the data provided by Lampinen et al. (2006).[26] In the simulation model below, each hive contains a fixed number of foragers. At each time step, the idle foragers in the nest are sent to the source with the highest net gain ratio. The duration of each foraging trip can be obtained from equation 5 by setting the metabolic rate coefficients to 1:

$$C_s(i,t) = \frac{2d_i}{v} + \frac{LoadSize}{CollectionRate P_{i,t}/F_t} VisitDuration + UnloadDuration. \tag{6}$$

As a result, although foragers choose the source with the lowest energy cost, they may not choose the trip with the shortest duration.

[26]The duration and the time of bloom varies across varieties. The model is specified for the Nonpareil, the most common variety.

Since bees do not forage at night, all foragers return to the hive at the end of each day. In this model, bees always go to the most profitable patch, which would require that the scouts of the colony are able to detect instantly any source that becomes more profitable and that is not being currently foraged and that the information transmission channel between hive mates is perfect.[27] This assumption may lead to overestimation of foraging efficiency in heterogeneous or patchy landscapes. In commercial almond orchards the high densities of both blossoms and bees, as well as the extreme homogeneity of the landscape reduces this bias. At a density of two hives per acre, the $3,000$ foraging bees in a hive have to choose among about 38 trees.

We assume that there are no direct interactions between bees on or around flowers.[28] Nevertheless, their foraging patterns are interdependent since they forage and deplete common patches. This interdependence of foraging patterns prevents the derivation of closed form solutions and requires the use of numerical simulations.

The steps of a simulation run of the foraging model are as follows. At each period t, the bees present in the hive go to forage on the source with the smallest foraging costs. Each bee depletes the pollen stock on the visited source by the size of a load. The cost of foraging on all visited sources is updated and the simulation moves to the next time period. The bees that leave to forage during period t are not available to forage again until period $t + C_s$, where C_s is the cost of foraging in seconds given in equation 6. All bees are available to forage at $t = 1$. These

[27] I assume that scouts do not contribute significantly to pollen removal or deposition and that all hives have the same fixed population of scouts.

[28] Direct physical interactions among pollinators on or around flowers are relatively rare, especially when forage is abundant (Thomson, 2004). Greenleaf and Kremen (2006) document however that honey bees interacting with wild bees are more likely to move to other flowers. Also, when forage is scarce, bees of different hives may engage in honey theft.

steps are repeated at each period until the end of the day of foraging. Accordingly, the bee-time budget of the hive is what constraints the amount of pollen collected and the number of visits made. This time budget is the product of the number of foraging bees and the number of hours in the foraging season.

Simulation of foraging behavior in homogeneous landscape without depreciation

In order to get a sense of the patterns of foraging generated by this model it is useful to start with a single hive foraging in a one-dimensional landscape where forage is distributed homogeneously and only once at the beginning of the foraging period:

$$\forall i, P_{i,0} = P_0. \tag{7}$$

In addition, the pollen does not depreciate and therefore, at each source the pollen stock is determined by the following equation of motion:

$$P_{i,t+1} = P_{i,t} - H_{i,t}, \tag{8}$$

where $H_{i,t}$ is the amount of pollen extracted by bees and is equal to the product of the number of bee visits $B_{i,t}$ by the size of a load $LoadSize$.

Figure 1 represents the spatial distribution of bee visits in panel (a), the cost of foraging in panel (b), and the stock of remaining forage in panel (c). The dashed line in each panel represents the profile of each variable at the beginning of the simulation period $t = 0$ and the continuous line the same profiles at the end $t = T$. The small square near the center of the space axis x represents the location of the hive. At $t = 0$, no visits have been made, the amount of pollen is constant across space and equal to P_0, and the bee visit profile is flat and equal to zero. As

a result, collection costs, which are the second term in equation 5, are constant across space. The flight cost term in equation 5 is a linear function of the distance from the hive to the source d_i. Flight costs, and consequently full foraging costs C_m have a "v" shape. The "v" shape of foraging costs is shown in panel (b) of figure 1.

The first bee to look for a patch to forage will forage as close as possible to the hive. As pollen is depleted from close sources, the collection costs for these source will increase until their total foraging costs equal those of more distant sources which have a lower collection cost but a higher flight cost. The hive will deplete pollen so that all sources in its foraging area have the same marginal foraging costs. Heuristically speaking, the "v" shape of the foraging cost profile in panel (b) will "fill in" like a tub. This process will continue until bees run out of time. In figure 1, the boundaries of the foraging range at the end of the foraging period are fixed by the number of foraging bees in the hive.

If we assume for a moment that metabolic rates are all equal to one, foraging costs are equivalent to time. In that case, the area of the gray triangle in panel (b) of figure 1 would represent the total time budget of the hive and would determine the foraging range of the hive at the end of the foraging period.[29]

The shape of the profiles of bee visits and pollen stocks depend on the specification of the collection costs that are described in equation 5.[30] In order to express the stock of pollen as a function of space within the foraging range of the hive, it is enough to note that the marginal cost of foraging is constant on

[29]By foraging range we mean the range of recruited foragers. Scouts may forage further and collect information on the quality and amount of forage in a much larger area.

[30]Note the that the pollen profile can be easily obtained from the bee visit profiles since each visit depletes the stock of the source by a fixed load. Also, these two profiles are not continuously differentiable at the hive location because the initial foraging costs are not differentiable either.

the foraging range and is equal to the marginal cost of foraging at the edge of the foraging range (see figure 1). At that point d^*, the pollen stock is equal to the initial value P_0, and according to equation 5 the marginal foraging cost is:

$$C_m^* = MR_f \frac{2d^*}{v} + MR_c \frac{LoadSize}{CollectionRate P_0/F} VisitDuration + MR_u UnloadDuration. \tag{9}$$

For every point within the foraging range $C_m(i,T) = C_m^*$. Using the expression of $C_m(i,T)$ from equation 5 and solving for the stock of pollen gives:

$$P_{i,T} = \frac{MR_c LoadSize B_i VisitDuration}{CollectionRate\left(C_m^* - MR_u\, UnloadDuration - MR_f 2d_i/v\right)} \tag{10}$$

which provides the profile of pollen in sources as a function of their distance to the hive. However, there are no closed form expressions for d^* and C_m^*.

Choice of foraging model and observed patterns of diffusion

The distribution of bee visits over space estimated by this model contrasts with those of models in the literature. Because the foraging behavior is coupled with the dynamics of forage, the model generates visit profiles that cannot be generated with diffusion models that take forage as fixed and given. However, the choice of model specification hinges on assumptions about the foraging behavior of pollinators, which vary across species. Distinguishing empirically the validity of alternative models with a single hive or other pollinator nest is difficult because the precise shape of the visit profile depends on parameters and function specifications that are hard to estimate. For instance, if a stochastic error is added to our model to account for the imperfection of information transmission among bees in a hive, the

profile of bee visits generated by our model is difficult to distinguish from a fully random diffusion model without forage dynamics.

Yet, when several hives or nests have overlapping foraging ranges, the distributions of foraging efforts in space from alternative models are easier to distinguish. Figure 2 shows the profiles for bee visits and forage stock in a landscape with three hives. When one hive extracts forage from a location that is within the foraging range of another hive, it alters the profile of foraging costs of this other hive. For instance, Hive 1 in figure 2 extends its foraging range further to the left in the presence of Hive 2 because forage is depleted more rapidly in the area where foraging ranges overlap. These interactions among hives through the depletion of a common forage make the profiles of bee visits non-additive. That is, the number of visits received by each source when all hives forage simultaneously is not the sum of the visits resulting from the foraging of each hive independently. In contrast, models of pollinator foraging that do not couple the allocation of foraging effort with the density of forage yield in contrast additive profiles of visits. Gary, Witherell, and Lorenzen (1978) use capture-recapture techniques to map the distribution of foraging efforts of hives in alfalfa fields. The patterns they observe are consistent with the non-additive profile predictions of our model. Experiments such as those of Gary, Witherell, and Lorenzen (1978) are relatively rare and have not been carried out for almonds. In particular, they require the measurement and mapping of all hives present in a relatively large area and of all the forage available to the bees.

Coupling foraging with blossom development

This section combines the model of foraging behavior developed above with a model of blossom development in almonds. In the previous simulations, the results of which are represented in figures 1 and 2, the stock of pollen available for foraging is released once at the beginning of the foraging period and only decreased as a result of extraction by bees. Here, the dynamics of forage are more complex and reflect the different stages of the development of almond blossoms. The pollen is released progressively during the bloom and some of the pollen can be lost if left on the blossoms for too long. In addition, the pollination effect of bee visits on nut set is tracked. The estimated number of pollen grains deposited during bee visits is used to calculate yield as a function of the distribution of bee visits in time and space.

The patterns of almond phenology can be interpreted along arguments similar to those used above for the foraging behavior of honeybees.[31] This section, however, does not analyze the trade-offs of pollination for almond trees and the modeling of the development of blossoms is descriptive. A more complete analysis of the trade-offs of pollination, which requires the analysis of trade-offs for both plant characteristics and insect behavior, is a promising extension of this study.

The next two sections describe the phenology of almond bloom and the way this dynamic phenomenon is represented in the model. The figures of these sections and their interpretation are sufficient to provide an understanding of how the progression of bloom is modeled and the equations used for computation do not provide additional intuition. Appendix provides a description of the variables, equations, and parameter values which can be used to replicate the numerical

[31] Phenology is the study of periodic biological events in relation to seasonal climate variations.

simulations which results are discussed in section below. This almond pollination model draws on DeGrandi-Hoffman, Roth, and Loper (1989) who develop a simulation model of cross-pollination and nut set for almonds that they calibrate on experimental data.

Blossom development and blossom cohorts

On a commercial almond tree, each blossom has a lifespan of about five days starting at the opening of the blossom and ending when petals fall.[32] The stigmas are receptive to pollen deposited by bees during these five days. However, the probability of a successful fertilization by the deposited pollen decreases with the age of the blossom as well as with the time of opening of that particular blossom relative to bloom progression.[33] The pollen contained in the anthers of blossoms is released in the mornings of the first couple of days after opening.[34] The pollen that is not collected during the day by bees is generally lost before the following morning, either because of the wind or to other insects.[35]

All blossoms on a tree do not open simultaneously and a given tree can hold opened blossoms for a duration of ten to twenty days. The proportion of open blossoms through time follows a curve with a bell shape.[36] The exact shape of this curve of opened blossoms varies across almond varieties as well as with weather conditions. DeGrandi-Hoffman, Roth, and Loper (1989) model the progression of bloom as a function of cumulative degree days. In this model, weather conditions are constant throughout bloom and each day is an average day in terms of degree

[32]Source: Robbin Thorp, Thomas Gradziel, personal communication.
[33]Source: McGregor (1976) and DeGrandi-Hoffman, Roth, and Loper (1989).
[34]Source: Robbin Thorp, Eric Mussen, personal communication.
[35]Source: Robbin Thorp, personal communication.
[36]See for instance Degrandi-Hoffman et al. (1996) or DeGrandi-Hoffman, Roth, and Loper (1989).

days. Under this assumption, the progression of bloom can be simulated in terms of time or degree days. For clarity, the model is presented in terms of days. Section discusses the how the model can be extended to include variable weather conditions which requires the progression of bloom to be simulated using degree days as in Degrandi-Hoffman et al. (1996).

In this model, each tree has a fixed number of blossoms (see table A.2). All blossoms last five days and release the pollen contained in their anthers on the first two days in equal quantity. All blossoms are assumed to have the same number and quality of grains of pollen. This model tracks the effects of both age and vintage on receptivity by dividing the blossoms of each almond tree in ten cohorts. The number of blossoms in each cohort is determined so that the cumulative number of opened blossoms is similar to what is observed by Degrandi-Hoffman et al. (1996) and DeGrandi-Hoffman, Roth, and Loper (1989).[37] Panel (a) in figure 3 shows the proportion of blossoms opened on each day of the bloom, as well as the contribution of each of the ten cohorts to opened blossoms. The amount of pollen released on each patch each morning is proportional to the number of blossoms opening that day or the day before. Panel (b) in figure 3 shows the corresponding amount of pollen released each day. Throughout the day, no additional pollen is released and at night. The pollen that is left on blossoms is lost.

Because all the pollen that is released one day is either collected by bees or lost during the night makes each day of the bloom independent in terms of foraging costs for bees. The only stock that is conserved from day to day is the pollen deposited on blossoms. As a result, each day of the bloom can be considered as an independent foraging period as described and simulated in section above.

[37] See section in appendix for details.

The amount of pollen available for foraging and the number of blossoms opened varies from day to day however, following the progression of bloom described in figure 3. Throughout each day, bees forage the pollen released by the blossoms on that morning.

Pollen deposition, nut set, and yield

While foraging, bees both collect and deposit grains of pollen. In the model, the number of grains of pollen deposited for each visit is fixed and equal to 30 as measured by Thomson and Goodell (2001). Recall from section that one foraging trip can involve the visit of several blossoms. A blossom sets nut when the sum of the number of pollen grains deposited throughout the blossoms's life, weighted by the receptivity at the time of the deposition is larger than the number of grains required for nut set. The receptivity of blossoms decreases as described in table A.3, in which values are calculated from DeGrandi-Hoffman, Roth, and Loper (1989).

To the best of our knowledge, no dose-response function of nut set to the number of pollen grains deposited has been estimated for almonds.[38] In this model nut set requires a minimum of 80 pollen grains and the dose-response function is a step, or Leontieff function. Past the threshold of 80 pollen grains the marginal increase in nut set is zero. In appendix , we test the sensitivity of the simulation results to both changes in this threshold value and to the specification of the dose-response function. The range of values and specifications tested is wide enough to include the empirical estimates for other crops (Cane and Schiffhauer, 2003) as

[38]Mitchell (1997) estimates a dose-response function of fruit set to pollen deposition for mustard and Cane and Schiffhauer (2003) for cranberries.

well as the number of pollen grains used in hand-pollination experiments (Yi et al., 2006).[39]

An important additional requirement for nut set in almonds is that some of pollen deposited must be from a different variety than the one pollinated. All known varieties of almonds are self-incompatible. Although the model can track two or more pollen types, the details of pollen transfers by honey bees are complex and have not been fully quantified yet. Therefore the results presented here assume that cross-pollination is not a limiting factor. Modeling cross-pollination requires the specification of the relationship between the probability of nut set and the numbers of grains of pollen from compatible and incompatible varieties deposited on blossoms. This relationship is not fully understood yet. Furthermore, the mixing of pollen from different varieties can occur either in the hive or from individual bees foraging on different varieties during the same foraging trip or during successive foraging trips. The simplifications of only tracking one type of pollen are more innocuous if most of the pollen transfers happen in the hive, which is the hypothesis favored by current experts (Gloria DeGrandi-Hoffman and Robbin Thorp, personal communications).

In the model, once the number of blossoms setting a nut has been estimated, the proportion of almond nuts that drop after bloom is calculated using the empirical equation estimated by DeGrandi-Hoffman, Roth, and Loper (1989) which provides the number of nuts per tree that remain on the trees. The nut set is finally

[39]Hand pollination corresponds with the maximum grains of pollen that can be deposited on a stigma.

converted into yield assuming 350 nuts per pound.[40] The values of the parameters used in the numerical simulations are presented in table A.2.

Summary of the simulation steps

One simulation run is a repetition of fourteen foraging periods which correspond to each day of the bloom. At the start of each foraging period, the blossoms at each source open, age, and release pollen as described in figure 3. Then, bees forage until they run out of time. Each time they visit a blossom, they both collect and deposit pollen. At the end of each day, or foraging period, the pollen that has not been collected is lost. In addition, all bees return to the hive. When a blossom has been open for five days, the number of pollen grains deposited by bees on its stigma during these five days is compared to the pollination requirement to determine whether the blossom sets nut. At the end of bloom, the number of blossoms that have set nut is used to calculate the yield.

Result of the simulation of foraging and pollination

The function which describes the relationship between almond yield and hive density can be obtained by running a series of simulations as described above, varying only the number of hives per acre of orchard. This section presents the results of that simulation and explains how yield depends on hive density according to this model in terms of foraging and pollination. The implications of the simulation results for the economics of almond pollination are left for section , which follows.

[40]The number of nuts per pound depends on the size of kernels which vary across varieties as well as according to water and nutrient application. DeGrandi-Hoffman, Roth, and Loper (1989) report a range of 319 to 396 nuts per pound, while Traynor (2001) estimates 350.

Before looking at the estimated yield curve, it is useful to note that with the parameters of commercial almond orchards, foraging bees spend most of their time on visits and very little flying from and to pollen sources. At densities of two hives per acre, the foraging range of hives is within 104 feet of the hive. With a flight speed of 19.7 feet per second (6 meters per second), bees can cover the distance of the longest foraging trips in less than 6 seconds. Even when hives are not distributed completely homogeneously in orchard, the flying part of foraging trips represent a very small fraction of the time budget of bees. An important consequence of this fact is that all trees receive about the same number of visits, independently of their proximity to the nearest hives. As a result, nut set and yield are homogeneous in space, as long as the trees are similar enough in terms of number of blossoms and other characteristics which affect foraging and nut set.

Figure 4 shows yield per acre as a function of hive density corresponding to the default parameter values shown in table A.2. The maximum yield that can be obtained is of $3,550$ pounds per acre, which requires 1.6 hives per acre or more. For densities between 0 and 1.5 hives per acre, the yield increases rapidly and by steps. The value of the maximum yield is comparable to what is considered a good yield according to some growers (personal communication) but is much higher than the average value of $2,000$ pounds per acre reported in variety trials or statistical data.[41] Several factors can explain the difference.

First, the maximum number of nuts per tree depends directly on the number of blossoms per tree, which varies across varieties, tree age, and water and nutrient availability. The simulation uses the value of $25,000$ blossoms per tree which may

[41] See for instance Lampinen et al. (2006), or the 2009 California Almond Forecast, from NASS, USDA.

be an optimistic estimate for the average. Appendix presents the results of the sensitivity analysis of the results to this and other parameters.

Second, the nut drop that occurs after bloom may be underestimated in the model. The equation for nut drop is drawn from Degrandi-Hoffman et al. (1996) who calibrate it on experimental data. Nut drop can vary across years and orchards and therefore the nut drop equation estimated in Degrandi-Hoffman et al. (1996) may not represent average conditions.

Finally, variation in planting densities may result in variations in the number of blossoms per acre. The discrepancy between the estimated maximum yield and observed yields is not, however, a limitation for the validity of the model. The central result of the simulations is the shape of the yield function, which is discussed below. This discrepancy between yields is also carefully dealt with in section so as to not overestimate marginal revenue.

In order to understand the pattern of the simulated yield curve it is useful to superimpose it upon the pattern of cohort nut set. In figure 5, the contribution of each cohort to the total yield for each value of hive density is represented by horizontal bars labeled with the number of each cohort. As hive density increases, more cohorts are successfully pollinated. Above 1.6 hives per acre, the blossoms of all cohorts set nut. Recall that since there is no spatial gradient of nut set, changes in yield per acre cannot be explained, for example, by changes in the proportion of trees that fully set nut. For a given hive density, all trees set the same number of nuts and changes in yield are caused by changes in the number of cohorts that are successfully pollinated.

In figure 5, the first cohort to fail is the last cohort to open, or cohort number 10. This is the result of the fact that the receptivity of this cohort is the

smallest of all (see table A.3) combined with the fact that for the last three days of that cohort's life, no pollen is available and bees do not forage. Also, this cohort has to compete for bees in the first days opening with cohorts of larger size. As the density of hives is reduced, more cohorts fail in inverted order of opening.

This pattern is not maintained for all the combination of parameter values of the sensitivity analysis as listed in table A.2. Sometimes, the first cohort to fail is the fifth or sixth to open. This happens because blossoms of these cohorts have to compete for bees with a larger number of blossoms than cohorts that open early or late, as can be seen in figure 3. No matter which cohort fails first, the first drop in yield to occur as hive density is reduced, is determined by the number of blossoms in that cohort. The fact that the entire cohort is lost at once is dependent on the specification of the dose-response function of nut set to number of pollen grains deposited, which for figure 5 is a step function. In appendix , figure B.1 shows that a smoother yield function is obtained for a continuous and stepwise linear dose-response function.

The shape of the yield function simulated by the model depends on how blossoms are distributed among cohorts. If all blossoms open on the same day and belong to a single cohort, the density of hives required for a full nut set is higher than if blossoms open over time. In addition, yield is a step function when there is only one cohort.

Simulated marginal revenues and the rule of thumb

The revenue per acre and the marginal revenue per acre as a function of hive density can be obtained by multiplying the yield of figure 4 by the price of almonds. Figure

6 is based on a price of \$1.73 per pound, which is the price averaged over the years 2001 to 2008.[42] The marginal revenue is calculated as the slope of the total revenue.

The central result of this simulation is the shape of the marginal revenue curve. In figure 4, the marginal revenue per additional hive is equal to about \$1,000 per acre at a hive density of 1.6 and falls to zero for any higher density. This almost vertical drop in marginal revenue corresponds to the failure of nut set for the last cohort. As noted before, the maximum yield simulated in the model is almost twice what is reported by growers. However, even dividing the marginal revenue by two and assuming \$500 per acre for the marginal hive, this drop is large enough to make the production function of almonds one of fixed proportions in hives over the ranges of almond and hive prices of the last couple decades. Recall that pollination fees for almonds have ranged from \$35 to \$140 per hive between 1995 and 2008 (see table 2).

Contrary to the shape of the marginal revenue curve, the simulated values of the marginal revenue function are not robust enough to provide a reliable estimate of the optimal hive density. As shown in appendix , the optimal hive density according to the simulation model is not robust to uncertainty in parameter values. The 95% confidence interval for the position of the vertical drop in marginal revenue ranges from 0.52 to 2.88 hives per acre with a median of 1.45.

Given this range of the uncertainty, the difference between the 1.6 hives per acre of the simulation model and the 2 hives per acre cannot be interpreted in terms of the economic behavior of growers. Furthermore, two factors which are not taken into account in the model may account for some of that discrepancy. The first is the effect of weather variability. Since the simulated revenue is not linear,

[42]Source:2009 California Almond Forecast, NASS, USDA, available at http://www.nass.usda.gov.

allowing the daily duration of foraging to be stochastic would result in a higher optimal hive density than with the fixed value used in the simulation above. The second factor is the cross-pollination requirements, which we have assumed here to be non-limiting.

The simulation model provides support for the hypothesis that almond production displays fixed proportions with respect to honey bees. However, it also brings forward additional questions regarding the economics of pollinator use.

First, the optimal hive density is sensitive to parameters that are susceptible to vary across orchard and throughout the life of a given orchard. It is precisely because the production function displays fixed proportions that these variations should be observed across orchards and time. Yet, the rule of thumb discussed above, as well as the recommendation of experts, do not take these variations into account.

Second, honey bees spend very little time flying according to the simulation model of commercial almond pollination. This is due to the fact that at the hive and blossom densities of commercial orchards, the flight speed of bees is very large relative to the size of the foraging range of beehives. As a result, hives spread their foraging effort and the pollination services they provide evenly in space. Therefore, the relevant hive density for any particular orchard depends on the number of hives placed in surrounding orchards as well. In addition to raising the possibility of externalities among growers, this diffusion makes it more difficult for individual growers to evaluate and even more, control, the actual number of bees that are pollinating their crop.

Finally, as pollination fees become more expensive, growers have an incentive to substitute their management time for bees. The development of quality standards

for hives, the adoption of new planting patterns that increase pollen transfer, and the development of quantitative tools that predict yield as a function of bee density are some of the visible outcomes of this trade-off between management and bee time inputs.[43]

Conclusion and further work

A simulation model such as the one developed in this paper cannot replace the empirical estimation of the changes in pollinator uses for crop production with changes in input and output prices. However, it does shed some light on the nature of the production function of crops. In the case of almonds, the simulation model supports the fixed proportion hypothesis. In addition, the model provides valuable insights for the development and implementation of empirical estimation.

First, the simulations show that hive densities need to be measured with enough precision to track changes in forager populations. Frame counts, which have not been collected in the past, might be required in order to capture variations in pollinator use. Because time series data with frame counts are not available, cross-sectional data may be the only feasible option.

Second, the model reveals the sensitivity of optimal hive densities to orchard parameters such as weather. These parameters are susceptible to vary in cross-sectional data and therefore may provide a useful identification strategy for econometric estimations of input demand elasticities.

Finally, the simulation model, which is spatially explicit, may be used to refine sampling strategies that take into account the diffusion of bees across orchards.

[43]The ARS of the USDA and the Almond Board of California are developing a web version of the almond pollination model in DeGrandi-Hoffman, Roth, and Loper (1989).

The main contribution of this paper to the literature on pollination lies in the integration of a spatially explicit foraging behavior model with a biological model of almond phenology. Yet, the model does not account for many of the behavioral adjustments that have been observed in hives. In fact, many of the fixed parameters have been shown to vary in response to changes in the availability of forage and of state variables of the hive.

For example, the value to the hive of a pollen load is constant throughout bloom in this model. Seeley (1995) observes that pollen is usually stored in limited quantities as opposed to nectar. As soon as the stock of stored pollen reaches a certain threshold, the hive reduces its effort towards pollen collection. During almond bloom, pollen collection is high and so is consumption since hives are building their worker population back after the winter. Whether the quantity of pollen stored remains on either side of this threshold throughout the bloom might determine whether the effort allocated to pollen collection is constant, which is what the model here assumes.

A second behavioral adaptation could play an important role both on the number of visits and on the amount of pollen collected. Goulson, Hawson, and Stout (1998) find that honey bees use odor cues to signal to themselves and their hive members which blossoms contain less pollen than average. Such a mechanism would greatly increase the foraging efficiency of bees compared to our estimations and would reduce the number of visits significantly by the same token. Developing a fully flexible economic model of foraging is however challenging because parameter values are difficult to obtain due to the complexity of a hive as a system.

The simulation results presented in section show that the distance-quality trade-off that the study of waggle dances has revealed may not be the most

important mechanism for foraging efficiency gains in dense and spatially homogeneous landscapes. In such situations, odor cues left on individual blossoms can yield higher foraging efficiency gains. Whether the amount of energy spent by hives on each of these information sharing channels varies is unknown, and additional mechanisms may turn out to be predominant in yet other forage conditions.

Finally, the dynamics of forage and the changes in the foraging behavior of individual bees are important determinants of the number of visits received by blossoms when bee density is high relative to forage density. Further research will be required to refine the specification of the costs of foraging with diminishing forage density. To the best of our knowledge this is the first model that explicitly couples the foraging behavior of pollinators with the incentives provided by a dynamics stock of forage. Extending this type of model for other species of pollinators is a promising lead into understanding the interactions between wild and managed pollinators.

This paper studied two embedded behaviors. Some patterns of the economic behavior of crop growers can be understood in the light of the economic behavior of foraging beehives.

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Table 1: Shares of hive rentals in operating costs for almonds from 1970 to 2008

Year	Hive Rental Price *dollars per hive*	Almond Price[a] *dollars per pound*	Input to Output Price Ratio	Hive Density[b] *hives per acre*	Recommended Frames *number of frames per hive*	Cost Share of Pollination[c] *percentage*
1970	4	na	na	2.0	na	2.0
1992	30	1.30	23.1	2.0	na	3.4
1997	40	1.56	25.6	2.5	5+	6.4
1998	40	1.41	28.4	2.5	5+	6.7
2001	50	0.91	54.9	2.5	na	9.7
2002	45	1.11	40.5	2.5	5+	7.9
2003	55	1.57	35.0	3.0	6-7	7.6
2006	125	2.06	60.7	2.0	5+	14.6
2007	140	1.75	80.0	2.5	5+	15.0
2008	125	1.40	89.3	2.0	6+	10.2

Source: Author's calculation with data from University of California Cooperative Extension, Cost and Return Studies, years 1938 to 2008, available at http://coststudies.ucdavis.edu/. Note: Pollination costs were omitted in studies from 1938, 1950, and 1954.
Item numbers in order: AM-VS-70, AM-VN-92-O2, AM-VS-97, AM-VN-98-1, AM-SV-01, AM-VS-02-1, AM-VS-03-2, AM-VN-06-1, AM-VN-07-O-R, and AM-VS-08-1.
[a] Almond prices come from agricultural price reports of the United States Department of Agriculture, National Agricultural Statistics Service. [b] The hive densities reported here are those found in the cost studies and are comparable to recommendations from other sources.
[c] The cost share of pollination is the share of the pollination fees in total operating cost, both per acre and excluding cash and non-cash overhead costs.

Table 2: Price, yield, and share of pollination costs in total revenues for almonds from 1995 to 2008

Year	Yield[a]	Price[a]	Pollination Fee[b]	Input to Output Price Ratio	Share of pollination in Total Revenue[c]
	pounds per acre	*dollars per pound*	*dollars per hive*		*percentage*
1995	890	2.48	35.41	14.3	3.2
1996	1,190	2.08	36.71	17.6	3.0
1997	1,720	1.56	38.59	24.7	2.9
1998	1,130	1.41	40.36	28.6	5.1
1999	1,720	0.86	41.43	48.2	5.6
2000	1,380	0.97	42.37	43.7	6.3
2001	1,570	0.91	45.01	49.5	6.3
2002	2,000	1.11	45.94	41.4	4.1
2003	1,890	1.57	51.99	33.1	3.5
2004	1,760	2.21	53.67	24.3	2.8
2005	1,580	2.81	72.58	25.8	3.3
2006	1,920	2.06	136.98	66.5	6.9
2007	2,240	1.75	140.00	80.0	7.1
2008	2,210	1.45	125.00	86.2	7.8

[a] Source: United States Department of Agriculture, National Agricultural Statistics Service, available at: http://www.nass.usda.gov/Statistics_by_State/California/Publications/Fruits_and_Nuts/.

[b] Source: California State Beekeepers Association pollination survey.

[c] This is the cost of pollination per acre divided by the revenue per acre which is equal to the product of yield and price. We assume a stocking rate of two hives per acre.

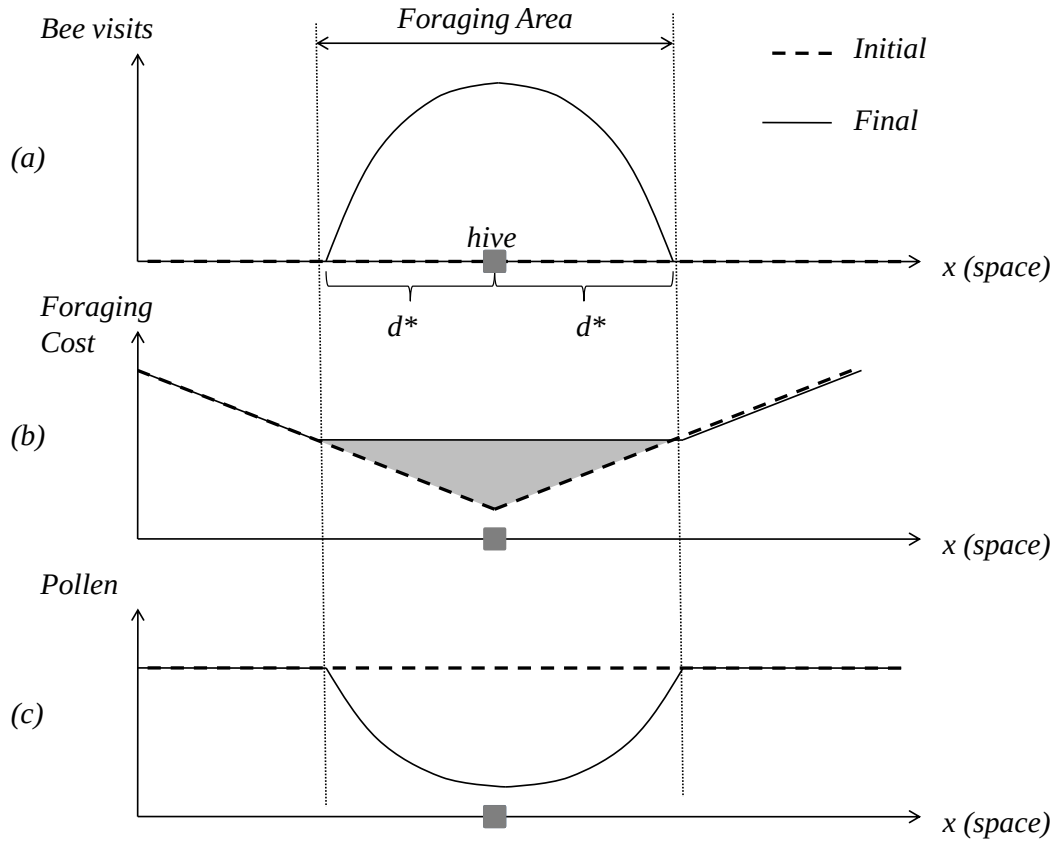
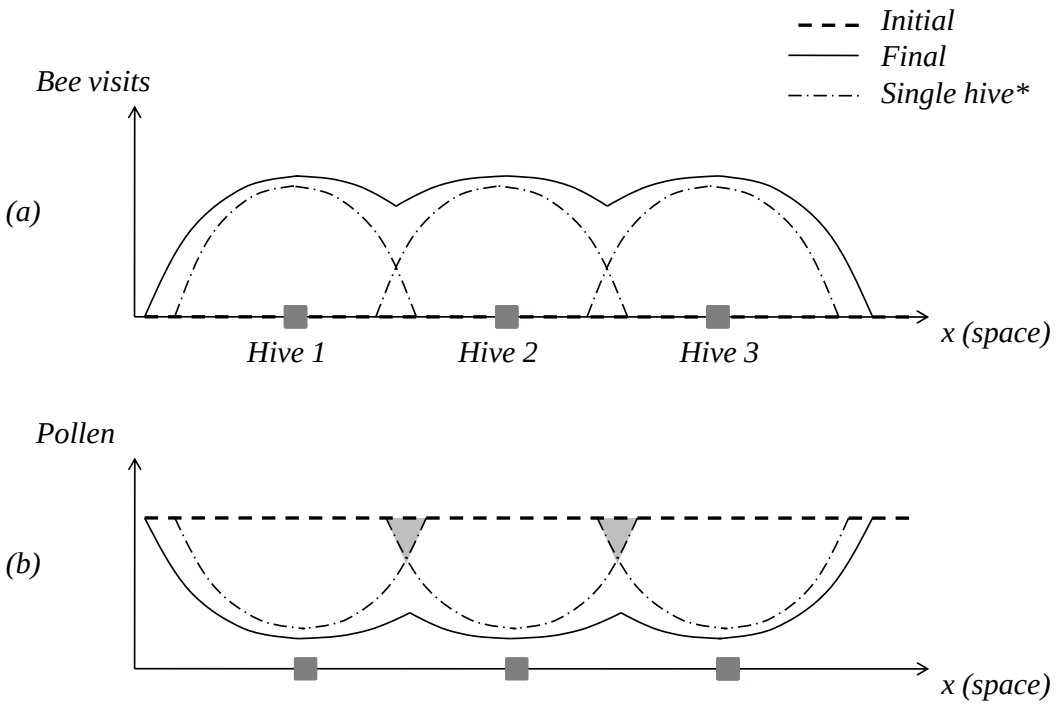
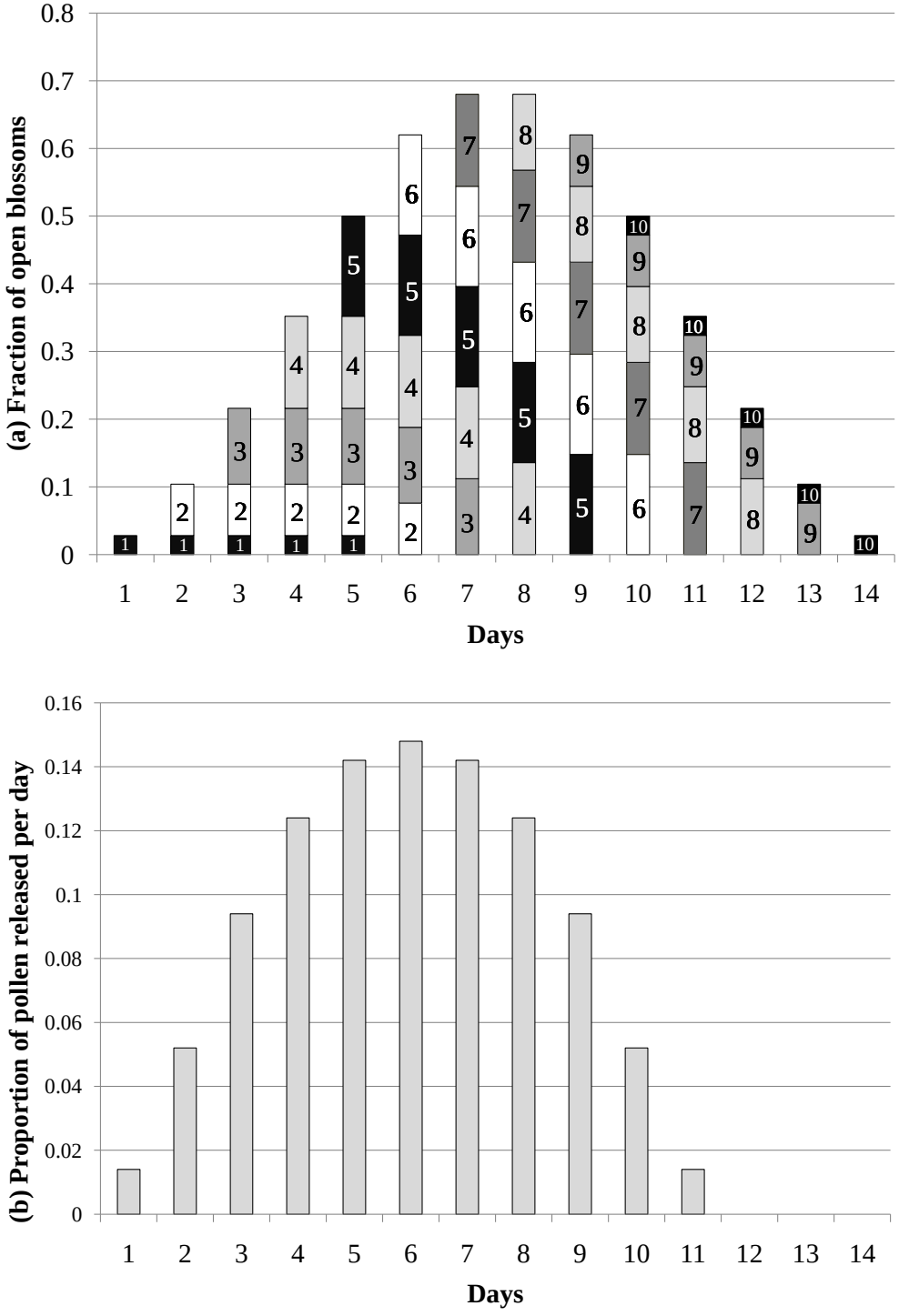


Figure 1: Profiles of bee visits, foraging costs, and forage stocks for a single hive with a homogeneous and non-depreciating forage distribution



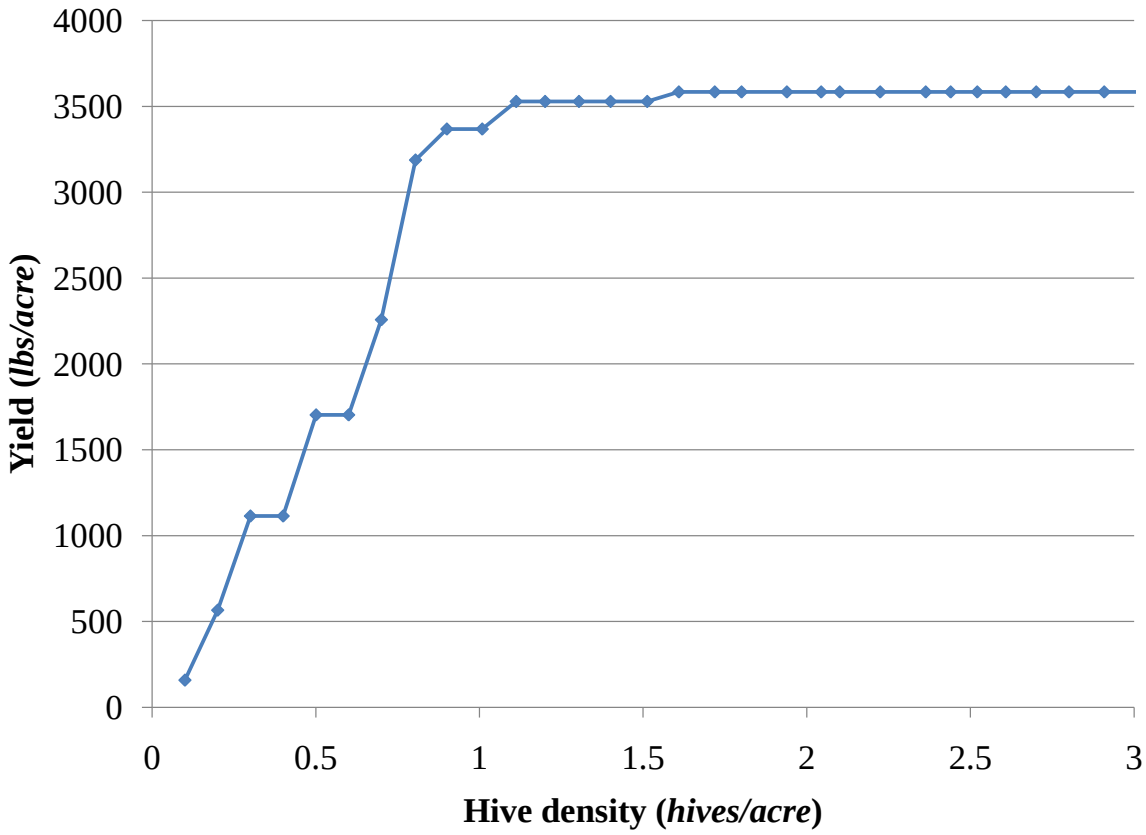
*The single hive profiles correspond to the profiles of each hive foraging without the presence of the other two hives.

Figure 2: Profiles of bee visits and forage stock for three hives with a homogeneous and non-depreciating forage distribution



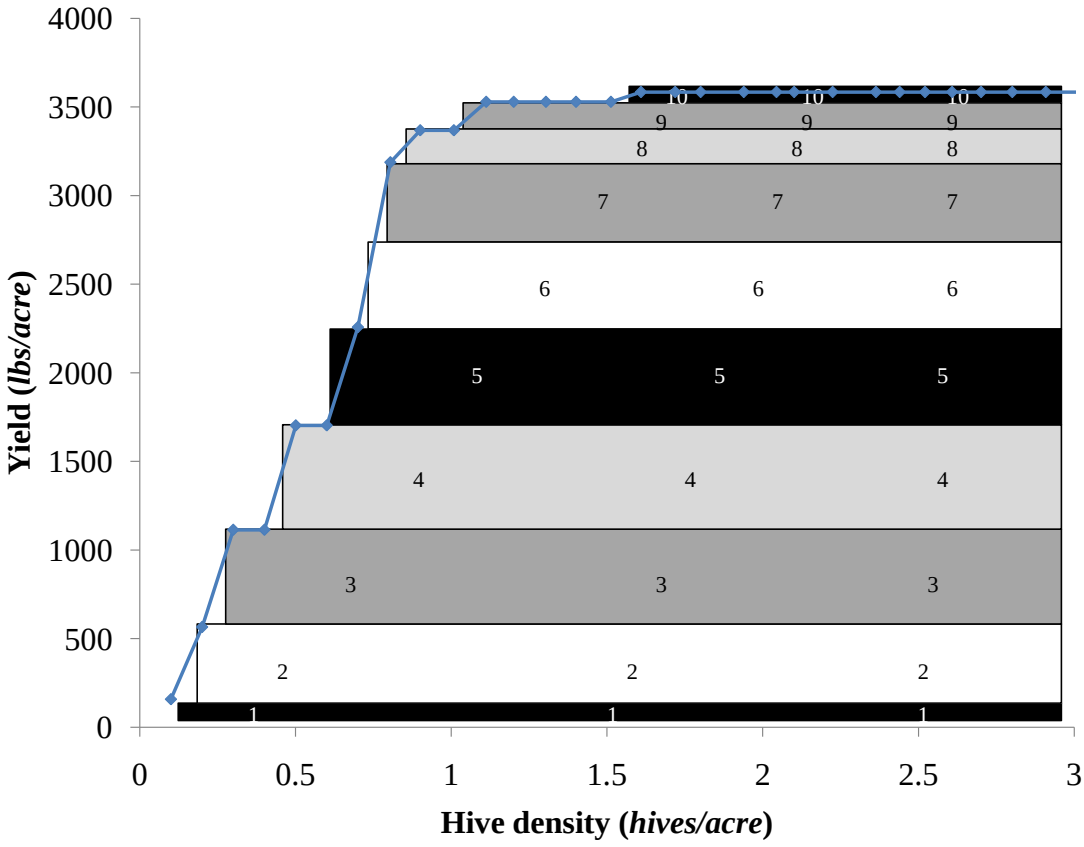
Note: The numbers inside the bars of panel (a) correspond to cohort numbers.

Figure 3: Development of blossoms by cohorts and release of pollen through bloom



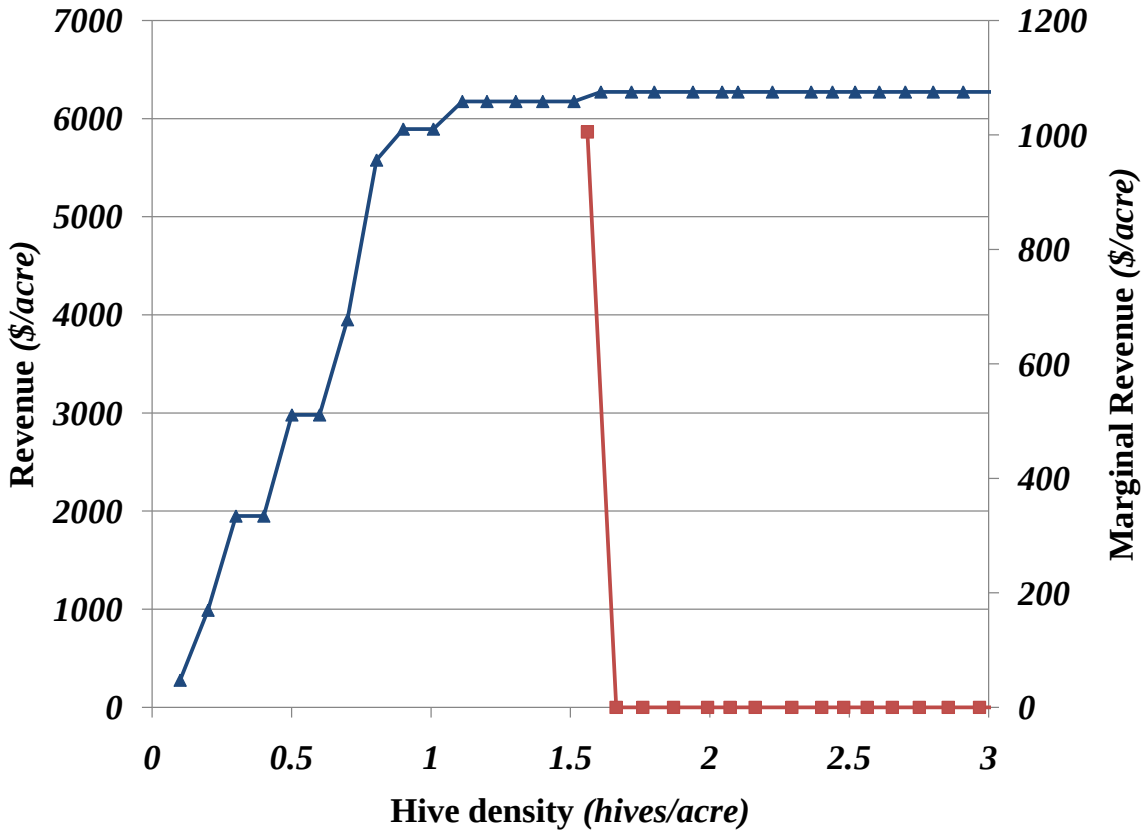
Note: A hive contains 3,000 active foragers.

Figure 4: Almond yield as a function of hive density



Note: The numbers inside the bars correspond to cohort numbers.

Figure 5: Almond yield and cohort success as functions of hive density



Note: A hive contains 3,000 active foragers.

Figure 6: Total and marginal revenues as functions of hive density

Appendix: Variables, parameters and equations of the almond pollination simulation model

Definition of indices and variables

This appendix presents the simulation model that combines foraging and almond nut set. Equations A.3 through A.15 describe how the foraging of bees and the development of blossoms are simulated for the entire duration of the bloom. The state variables and their indices are presented in table A.1. The values of the parameters used in the equations are collected in table A.2. Table A.2 also shows the range over which the parameters are varied in the sensitivity analysis.

For clarity, equations A.3 through A.15 correspond to simulations of the foraging of a single hive in an orchard. These equations can be extended to allow for the foraging and interactions of multiple hives. However a model for a single hive placed in the middle of a square orchard is sufficient. Recall from the description of the foraging model in section that the foraging ranges of hives do not overlap in this foraging model if hives and forage are distributed homogeneously, which is generally the case in commercial almond orchards.[44] Because foraging ranges do not overlap, it is sufficient to model one hive and provide it with a square over which to forage alone.[45] In other terms, the nature of the boundaries to the foraging range of a hive does not matter given the specific foraging model of section . Changes in hive density can be obtained by varying the size of the square orchard available to the foraging of a single hive.

[44] In almonds like in other crops, beekeepers place beehives on pallets which hold four hives. I discuss the effect of this grouping in section but I find that effect to be very small in the case of commercial almonds.

[45] Simulating an orchard stocked with multiple hives requires adding an index to track hives and increases computing time. It provides the same results as a single hive model as long as the landscape and hive distribution are homogeneous.

There are four central state variables in the model, three of which characterize the states of blossoms and pollen and one which tracks the availability of foragers in the hive.

First, the pollen available to visiting bees at each source is represented by the variable $P_i(d,t)$. The index i designates sources. The orchard is divided in square grid cells, each of which is considered to be one source. The distances between sources and the hive, d_i, are calculated at the center of each cell and the hive is located at the center of the orchard. I use d as the index for the days of the bloom, which lasts 14 days. Each day is divided in time steps of five minutes which are indexed by t. The number of hours during which bees can fly and forage is limited by the weather. Lampinen et al. (2006) provide the number of "good bee hours" per bloom season for the years 1996 to 2006. I use the average number of hours per day and assume that all days of the bloom are identical in terms of weather.

Second, the variable $F_{i,a}(t,d)$ represents the number of flowers of age a in source i at time t of day d. The index a refers to the age of blossoms and ranges from 0 to 6. Blossoms last five days. The first class, labeled 0, tracks the number of blossoms that are still closed whereas the last age class 6, is used to represent the blossoms that have already set nut.

Third, the variable $D_{i,a}(t,d)$ is the cumulative amount of pollen deposited on the blossoms of age a of source i at time t of day d.

Since the blossom variable $F_{i,a}(d,t)$ and the deposited variable $D_{i,c}(a,t)$ are only updated once a day, the index t can be dropped in both. In addition, it is useful to introduce the index c, which tracks to the cohort number. In this model, the blossoms of a tree are divided in ten cohorts and therefore c ranges from 1 to

10. For the first ten days of bloom, one cohort opens every day. As a result, on day $d = 1$, only blossoms of cohort $c = 1$ are open and they are of age $a = 1$. On the second day, $d = 2$, blossoms of cohort $c = 1$ are of age $a = 2$ and blossoms of cohort $c = 2$ are of age $a = 1$. This opening and aging of blossoms continues until the blossoms of the last cohort leave age $a = 5$. The relation between d, a, and c is that on day d, the blossoms of cohort c are aged $a = d + 1 - c$ (or still closed if $d + 1 - c$ is negative, and $a = 6$ if $d + 1 - c > 5$). Conversely, on day d, the blossoms of age a belong to cohort $c = d + 1 - a$. These relationships between blossom ages and their cohort number are useful to interpret figure 3.a in particular.

Finally, the variable $B(d,t)$ represents the number of foragers available in the hive at time t. Table A.1 summarizes the names, definitions, and ranges of both indices and variables.

Initialization of state variables

The first step of a simulation run consists in initializing the four state variables. All blossoms are closed before bloom starts and therefore:

$$\begin{aligned} \forall i,d,\ a = 0\ \ F_{i,a}(d) &= BlossomsPerSource, \\ \forall i,d,\ a > 0\ \ F_{i,a}(d) &= 0. \end{aligned} \tag{A.1}$$

Pollen has neither been released by blossoms nor deposited by bees, and accordingly:

$$\begin{aligned} \forall i,a,d\ \ D_{i,a}(d) &= 0, \\ \forall i,d,t\ \ P_i(d,t) &= 0. \end{aligned} \tag{A.2}$$

Since all bees are available to forage every morning, the bee variable is initialized as:

$$\begin{aligned} \forall d \;\; B(d,1) &= \mathit{BeeForagingForce}, \\ \forall d, t > 1 \;\; B(d,t) &= 0. \end{aligned} \tag{A.3}$$

Development of blossoms

At the beginning of each day, blossoms may open, age, and release pollen. For each of the first ten days of bloom, a new blossom cohort opens. The number of blossoms that open on a given day is determined by the proportion of blossoms in each of the 10 cohorts. In order to reproduce the bell curve pattern of bloom progression observed by Degrandi-Hoffman et al. (1996), I assume that the opening time of each blossom is an independent random variable which follows a symmetric beta distribution with parameters $\alpha = 2$ and $\beta = 2$. The deciles of the the beta distribution provide the proportion represented by each of the ten cohorts. The proportion of blossoms opening on the fourteen days of bloom are therefore

$$\Delta = [0.028, 0.076, 0.112, 0.136, 0.148, 0.148, 0.136, 0.112, 0.076, 0.028, 0, 0, 0, 0], \tag{A.4}$$

where the four last zeros reflect the fact that no blossom opens during the last four days of bloom. The sum of the element of Δ is equal to one. It is important to note that the cumulative number of open blossoms on each day of bloom is not Δ since blossoms remain open for five days.

The opening of new blossoms is expressed as:

$$\begin{aligned} \forall i, d, a = 1 \;\; F_{i,a}(d) &= \Delta(d) * \mathit{BlossomsPerSource}, \\ \forall i, d, a = 0 \;\; F_{i,a}(d) &= F_{i,a}(d) - \Delta(d) * \mathit{BlossomsPerSource}, \end{aligned} \tag{A.5}$$

where the parameter *BlossomsPerSource* is the number of blossoms per tree divided by the number of cells that cover a tree. Here, the definition of the space grid is such that there is one tree per cell and therefore $BlossomsPerSource = 25,000$. In figure 3.a, the size of the bars for each cohort is equal to the decile of the beta distribution multiplied by the number of blossoms per cell.

The aging of blossoms that are already opened is expressed as:

$$\forall i, 2 \leq a \leq 5, 2 \leq d \leq 14 \;\; F_{i,a}(d) = F_{i,a-1}(d-1), \tag{A.6}$$

which simply moves all the blossoms from one age class to the next. Recall that the variable for deposited pollen $D_{i,a}(d,t)$ is cumulative throughout the life of blossoms. Accordingly, pollen deposited on flowers of age d will be part of the pollen deposited on flowers of age $d+1$ one day later. The daily update of pollen deposited by bees is given by:

$$\begin{aligned} \forall i, d, a = 1 \;\; D_{i,a}(d) = 0, \\ \forall i, 2 \leq a \leq 5, 2 \leq d \;\; D_{i,a}(d) = D_{i,a-1}(d-1). \end{aligned} \tag{A.7}$$

The calculation of the number of blossoms that set nut is also performed every foraging day using the number of blossoms of age 5 and the pollen that has been cumulatively deposited on them throughout their lives. I assume that to set nut, blossom require that at least 100 grains of pollen have been deposited during the blossom's life. As shown below in equation A.15, grains deposited during the first days of the blossom are more likely to trigger nut set and the variable $D_{i,a}(d)$ represents cumulative discounted pollen grains. The number of blossom have net

nut on patch is updated according to the following equation:

$$\forall i, 2 \leq d, a = 6$$
$$F_{i,a}(d) = F_{i,a}(d) + \begin{cases} F_{i,a-1}(d) & if \quad D_{i,a-1}(d-1) \geq PollenRequirement \\ 0 & if \quad D_{i,a-1}(d-1) < PollenRequirement \end{cases} \tag{A.8}$$

where *PollenRequirement* is the number of required pollen grains for nut set. Given the lack of experimental data on the value of this parameter, I test the sensitivity of my results over a range of values in appendix . The effect of specifying a linearly increasing nut set function rather and step function is also discussed in the sensitivity analysis.

Release of pollen

In the model, blossoms release pollen during the first two days after opening and therefore, the amount of pollen available to bees at the beginning of each day is given by:

$$\forall i, d, a = 1 \;\; P_i(d,a) = \frac{PollenPerBlossom}{2}(F_{i,a}(d) + F_{i,a+1}(d)) \tag{A.9}$$

where the parameter *PollenPerBlossom* is the product of the average numbers of anthers per blossoms and grains of pollen per anther (see table A.2).

Simulation of a foraging day

This section describes how each day of foraging is simulated and how pollen is collected and deposited from and on blossoms. The foraging starts once the blossom and pollen variables have been updated as described in the equations A.5 through

A.7. For each time period t, which ranges from 1 to 48 (see table A.2), the following procedure is repeated until all the bees present in the hive at time t have left to forage, which can be written as:

$$B(d,t) = 0. \tag{A.10}$$

For each bee in the hive, the complete foraging cost in energy terms is calculated for the entire orchard according to equation 5 and the bee goes to the source i^* with the smallest cost:

$$i^* = argmax(C_m(i,t),i). \tag{A.11}$$

$C_m(i,t)$ is a function of the stock of pollen $P_{i^*}(d,t)$, and of the number of open blossoms $\sum_{a=1}^{5} F_{i^*,a}(d)$.

In order to determine the time when the bee will return from her foraging trip, the complete cost of the foraging trip in time $C_s(i^*,t)$ is calculated according to equation 6. The variable $B(d,t)$ is updated to reflect the fact that the bee is unavailable to forage again until time $t + C_s(i^*,t)$:

$$B(d,t+C_s) = B(d,t+C_s) + 1. \tag{A.12}$$

If $t + C_s$ is larger than 48 which is the end of the foraging day, the bee is not available to forage until the following morning and $B(d,t)$ is not updated.

At the chosen source i^*, the stock of pollen available for forage is depleted by the size of a load as the result of the bee visit:

$$P_{i^*}(d,t) = P_{i^*}(d,t) - BeeLoadSize. \tag{A.13}$$

In addition, the bee deposits pollen grains on the blossoms it visits.[46] The number of visits that a bee makes on a given source depends on the stock of pollen and the number of blossoms and is given by

$$\frac{LoadSize}{P_{i^*}(d,t)CollectionRate}\sum_{a=1}^{5}F_{i^*,a}(d).$$

For each of these visits, the bee deposits a fixed number of pollen on the stigmas of the blossoms. The average amount of pollen deposited per blossom is therefore:

$$\bar{D}=\frac{LoadSize}{P_{i^*}(d,t)CollectionRate}PollenDeposition \tag{A.14}$$

where *PollenDeposition* is the number of pollen grains deposited during each bee visit (see table A.2). With this specification, open blossoms of all ages receive the same number of visits and therefore the same amount of pollen. At each source, what determines both foraging costs and pollen deposition is the average ratio of pollen to blossoms and all ages are lumped together.[47] The variable for deposited pollen is updated according to:

$$\begin{gathered}\forall a\ \ D_{i^*,a}(d)=D_{i^*,a}(d)+\bar{D}F_{i^*,a}(d)R(c,a)\\ with\ \ c=d+1-a\end{gathered} \tag{A.15}$$

[46]Recall that I call foraging trip the round trip from and to the hive, whereas I call visit each stop on a new blossom. Hence, one foraging trip can involve one or more visits.

[47]This limitation could be the object of an extension however such extension would require additional information on the behavior of foraging bees at a patch. To the best of my knowledge, the behavior of bees in relation to the age and state of blossoms has not been quantified quantified. However, appendix shows that this averaging effect does not alter the simulation results significantly.

where $R(c,a)$ is the parameter that tracks the receptivity to pollination of blossom of cohort c when its age is a. $R(c,a)$ decreases when the age or cohort number of the visited blossom increases as shown in table A.3.

Once all days of foraging days have been simulated according to the steps described in this section, the yield in almonds is calculated. Note that during the last three days of bloom, no foraging occurs because no more pollen is released from the blossoms (see figure 3.b).

Calculation of yield, revenue, and marginal revenue

The number of blossoms that have set nut at the end of the bloom is given by $F_{i,6}(9,48)$. However, not all pollinated blossom will become nuts and the drop of nuts which occurs naturally between pollination and harvest must be taken into account to estimate yield. I use the equation for nut drop provided by DeGrandi-Hoffman, Roth, and Loper (1989). This equation calculates the proportion of blossoms that produce a nut at harvest from the proportion of blossom that are fully pollinated out of all the blossoms that open during the bloom:

$$N_i = \left[SN_i(0.057 + \exp(-\frac{SN_i}{2}) \right] F_{i,6}(9,48) \tag{A.16}$$

where N_i is the number of nuts at harvest on source i and SN_i is the proportion of blossoms that have set nut, or

$$SN_i = \frac{F_{i,6}(9,48)}{BlossomsPerCell}$$

. The specification of functional form and parameter values are those of DeGrandi-Hoffman, Roth, and Loper (1989). The nut set is finally converted into yield assuming 350 nuts per pound.[48]

The total revenue per acre is calculated using a price of \$1.73 per pound, which is the price averaged over the years 2001 to 2008. [49] The marginal revenue is then calculated as the slope of the total revenue.

[48]The number of nuts per pound depends on the size of kernels which vary across varieties as well as according to water and nutrient application. DeGrandi-Hoffman, Roth, and Loper (1989) report a range of 319 to 396 nuts per pound, while Traynor (2001) estimates 350.

[49]Source:2009 California Almond Forecast, NASS, USDA, available at http://www.nass.usda.gov.

Table A.1: Names and definitions of indices and variables of the almond pollination model

Variables		
Name	Definition	Unit
$P_i(d,t)$	Pollen available for forage	Grains of pollen
$D_{i,a}(d)$	Total amount of pollen deposited by bees on blossoms of age a	Grains of pollen
$F_{i,a}(d)$	Number of blossoms by age	Number of Blossoms
$B(d,t)$	Number of bees in the hive that are available to forage	Number of Bees
Indices		
Name	Definition	Range
i	Space	$[1,I]^a$
d	Foraging days	$[1,14]$
t	Time steps in a foraging day	$[1,48]^b$
a	Age of blossom	$[0,6]$
c	Blossom cohorts	$[1,10]$

[a] Although space has two dimensions, sources can be indexed with a single index once distances from hive to sources have been calculated and indexed according to i. Here I is the total number of sources and it is equal to the product of the dimensions of the space grid. It varies with hive densities since the area available to one hive for foraging varies with hive density.

[b] The number of time steps in a day is equal to the number of foraging minutes in a day divided by the time step. Here, there are 4 hours, or 240 minutes, in a foraging day and the time step is 5 minutes.

Table A.2: Values and sources of the parameters used for the simulation of almond yield

Biological Parameters				
Name	Value	Range	Unit	Source
Flight time per day	4	3-5	hours	Lampinen et al. (2006)
Bloom duration	14		days	Lampinen et al. (2006)
Blossoms per tree	25,000	20,000-30,000		Traynor (2001)
Anthers per blossom	32	25-50		Godini (1981)
Pollen grains per anther	1,500	1,000-2,000		Godini (1981)
Trees per acre	76			Traynor (2001)
Bee foraging force	3,000		bees per hive	E. Mussen, personal communication
Bee flight speed	6	4-8	$m.s^{-1}$	Seeley (1995)
Unloading time	120	60-240	seconds	Seeley (1995)
Bee load size	300,000	200,000-400,000	pollen grains	Traynor (2001)
Single visit duration	15	10-20	seconds	Thomson and Goodell (2001)
Pollen collection rate	.5	.3-.5	per visit	Thomson and Goodell (2001)
Pollen deposition	30	20-100	pollen grains per visit	Thomson and Goodell (2001)
Pollen requirement for nut set	100	30-200	pollen grains	Cane and Schiffhauer (2003)

Simulation Parameters		
Name	Value	Unit
Space grid definition	24	feet
Time grid definition	5	minutes
Number of blossom cohorts	10	

Table A.3: Estimates of blossom nut setting probability as a function of bloom period and blossom age

	Blossom age				
Cohort*	1	2	3	4	5
1	0.94	0.74	0.54	0.27	0.10
2	0.90	0.71	0.52	0.26	0.09
3	0.80	0.64	0.47	0.23	0.08
4	0.71	0.56	0.41	0.21	0.07
5	0.61	0.49	0.36	0.18	0.06
6	0.52	0.41	0.30	0.15	0.05
7	0.42	0.34	0.25	0.13	0.04
8	0.28	0.23	0.17	0.08	0.03
9	0.19	0.15	0.11	0.06	0.02
10	0.09	0.08	0.06	0.03	0.01

Source: Author's calculations from table 2 in DeGrandi-Hoffman, Roth, and Loper (1989). DeGrandi-Hoffman, Roth, and Loper (1989) provide nut set probabilities for 10 ages and 10 periods which are averaged in order to obtain the values for 5 ages and 10 periods used in the simulation model.

* Cohort c is the cohort which opens on day c of the bloom.

Appendix: Sensitivity analysis of the model of almond pollination

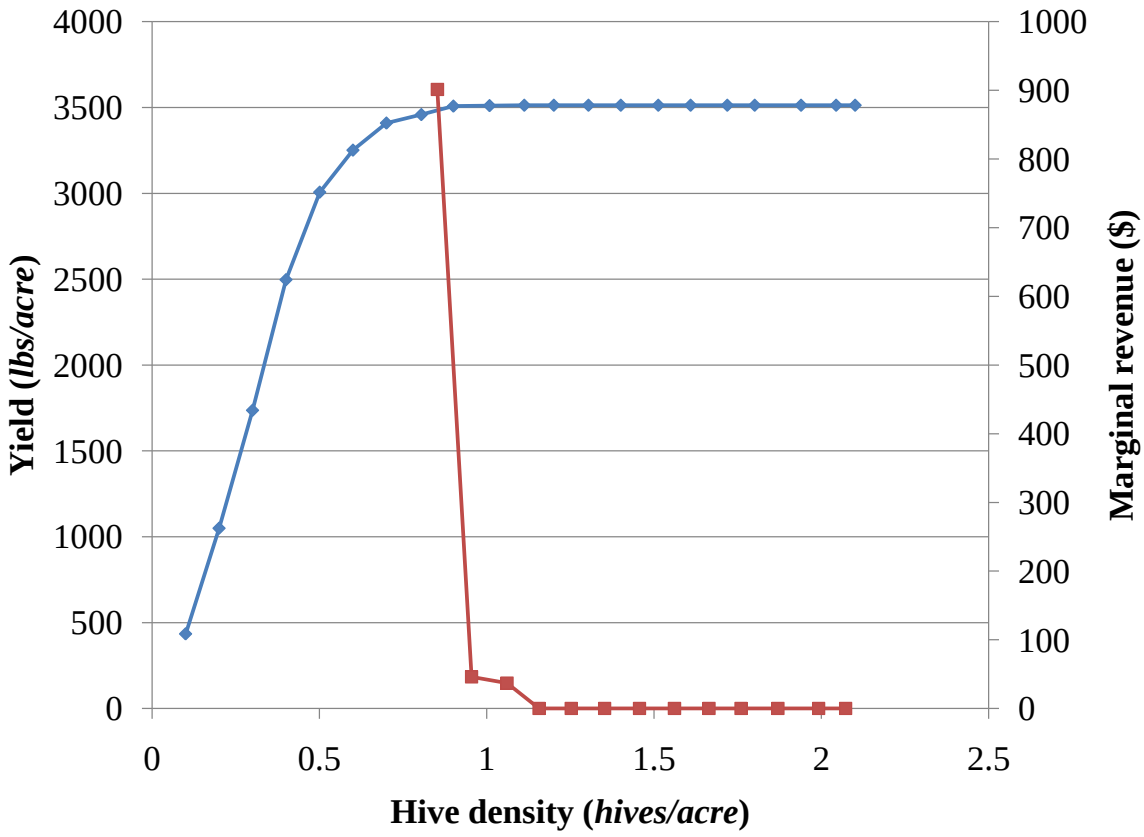
This appendix presents the results from sensitivity analysis of the almond pollination model.

Figure B.1 shows the effect of specifying a continuous and stepwise linear function for the response of nut set to pollen deposition. Instead of the step function described in equation A.8, the proportion of blossoms of a cohort that are setting nut is allowed to vary linearly between zero and one. This results in a smoothing of the yield function because cohorts can be partially successful in setting nut. However, the marginal revenue curve displays the same pattern as in the stepwise specification with a sudden drop in marginal revenue at .9 hives per acre. This analysis shows that the central result of the simulation is robust to addition of some degree heterogeneity within cohorts.

The second sensitivity analysis presented in this appendix concerns the values of the parameters of the model. Figure B.2 is obtained by sampling a thousand combinations of parameter values in the range reported in table A.2. The sampling is based on a uniform distribution on with support equal to the range of each parameter. All parameters with a range indicated in table A.2 are sampled simultaneously but without correlation. Once the yield for each hive density have been simulated for the thousand sets of parameter values, the average, median, and 95% confidence interval are calculated. Note that none of the curves in figure B.2 can be obtained as the yield function because the average, median, and 95% confidence interval are calculated for each hive density separately. Despite the relatively large variations in the yield function, the fact that the marginal revenue curve has an almost vertical section as shown in figures 6 and B.1 is robust to changes in parameter values. The hive density at which the marginal

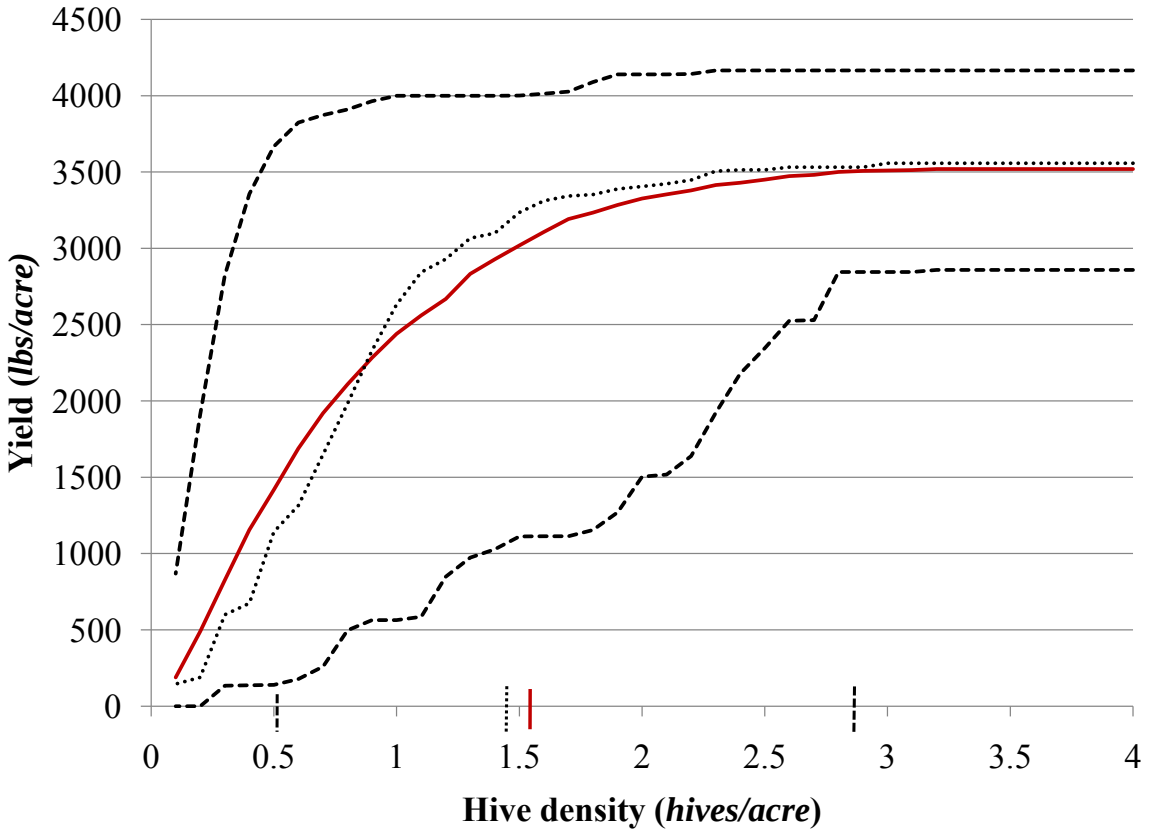
revenue drops suddenly depends however on parameter values. Figure B.2 shows the average, median, and 95% confidence interval for that hive density.

Finally, figure B.3 shows the sensitivity of the yield function to the size of the cells of the space grid. Given the large number of blossom per tree, each blossom cannot be tracked individually. The ideal number of grid cells per tree is equal to the number of blossom per tree. However, in the simulation presented in sections and , all the blossom of a tree are lumped together in a single cell. Figure B.3 shows that the result of the simulation are robust to changing the number of cells per tree. This robustness it due in particular to the fact that in the conditions of commercial almond orchards, bees forage homogeneously over space, and therefore do not establish a spatial gradient of nut set. This need not be the case for parameter values representing other crops or conditions.



Note: The nut set dose-response function for this yield curve is continuous and piecewise-linear. There is no nut set when less than 80 grains are deposited, full nut set for 120 or more grains. For 80 to 120 grains of pollen deposited, the fraction of blossom that set nut increases linearly from 0 to 1. The values of all the other simulation parameters are those given in table A.2. The marginal revenue is calculated with a price of $1.75 per pound of almonds.

Figure B.1: Yield and marginal revenue curve for an alternate nut set dose-response function



The parameters are sampled on the intervals reported in table A.2. The continuous line is the average yield, the dotted line the median yield, and the dashed lines the boundaries of the 95% confidence interval. The small vertical line on the horizontal axis show the average, median, and 95% confidence interval for the density at which the first cohort fails to set nut.

Figure B.2: Average and median yield and 95% confidence interval

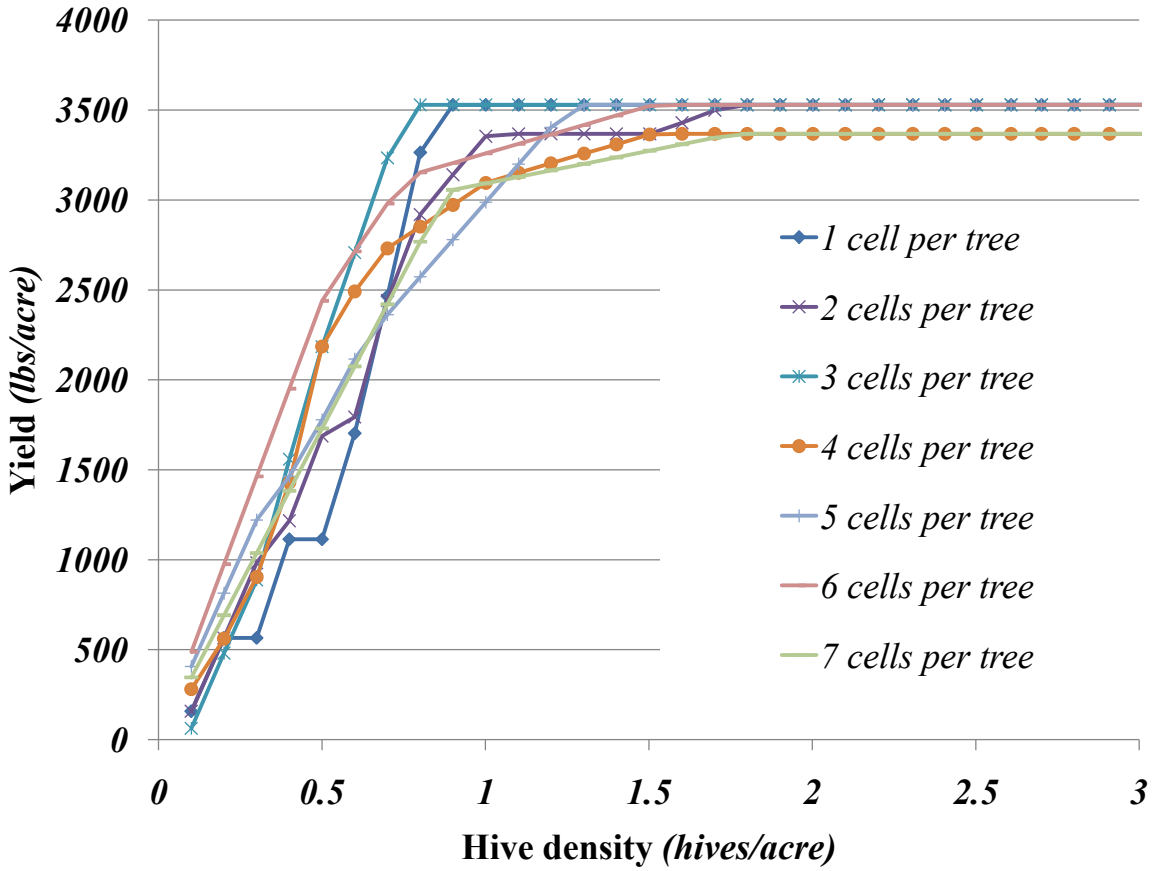


Figure B.3: Sensitivity of the yield function to changes in grid cell definition